



## Phylogenetic status of *Metarhinus pater* (Brontotheriidae: Perissodactyla) from Southern California and species variation in *Metarhinus* from the middle Eocene of North America

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PHYLOGENETIC STATUS OF *METARHINUS PATER* (BRONTOTHERIIDAE:  
PERISSODACTYLA) FROM SOUTHERN CALIFORNIA AND SPECIES VARIATION IN  
*METARHINUS* FROM THE MIDDLE EOCENE OF NORTH AMERICA

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**ABSTRACT**—In addition to its abundance in the middle Eocene of the Western Interior of North America, fossils of the brontothere *Metarhinus* are known from similar aged deposits in Southern California. Because of additional material from the Friars and Santiago Formations, San Diego County, California, *M. pater* Stock (1937), a dubious species formerly known from a single specimen, can now be differentiated from other nominal species of *Metarhinus*, *M. fluvialtilis* Osborn (1908), and *M. abbotti* (Riggs, 1912). Inclusion of *M. pater* into an analysis of brontotheriid phylogeny establishes *Metarhinus* as a monophyletic genus of uncertain origin. The three species of *Metarhinus* differ in the shapes of their nasals and the lengths of their nasal incisions, whereas other aspects of their skulls are undifferentiated. The majority of *Metarhinus* specimens lack species-diagnostic features and thus have unknown specific identities. At least two species co-occur wherever *Metarhinus* is abundant. We question whether these morphospecies represent population-lineage units (i.e., species), or if they are intraspecific variants possibly explained by ontogeny or sexual dimorphism. Dental wear stages, used as an age proxy, are uncorrelated with *Metarhinus* morphospecies. Likewise, variation observed within *Metarhinus* samples is inconsistent with sexual dimorphism. Coefficients of variation (CVs) suggest that the cheektooth dimensions of *Metarhinus* assemblages are more variable than monospecific referent samples, and that most assemblages are mixtures of two size-differentiated species. The persistent sympatry of *Metarhinus* species is a biogeographic pattern that appears to be atypical in comparison to other brontotheriids and could indicate an unusual case of sympatric speciation.

INTRODUCTION

Species are the fundamental unit of evolution (e.g., Cracraft, 1989; Claridge et al., 1997; Horvath, 1997; Barton, 2001; Gould, 2002; Sites and Marshall, 2004). The vast majority of fossil species are, by necessity, discovered and defined via morphological characters (Bruner, 2004; Forey et al., 2004), whereas extant species can be discovered and defined by a variety of criteria in addition to morphology, including molecular, ecological, behavioral, and reproductive criteria (Kimbel and Martin, 1993; Coyne and Orr, 2004; Dieckmann et al., 2004; Sites and Marshall, 2004; Bock, 2006). Fossil species are generally conceptualized as being equivalent to modern species, even though this may not always be the case because our ability to study fossil populations is extremely limited and it is significantly more difficult, if not impossible, to test whether or not fossil species represent distinct population-lineage units between which gene flow is absent or limited. Nonetheless, the assumption of extant and extinct species equivalence is an underpinning of paleontological studies about the evolution and diversification of life (Benton and Pearson, 2001).

Debates over species concepts and species-delimiting criteria (Wheeler and Meier, 2000) notwithstanding, a host of operational problems associated with the discovery and diagnosis of fossil species persist. For instance, only hard parts (e.g., skeletons, teeth, and shells) are preserved and most of the potential (soft-tissue) characters are, with rare exception, permanently lost. Even when species-diagnostic characters do involve hard

parts, identification of fossil material to the fundamental species-level is often difficult or impossible because the recovered specimens themselves are fragmentary and most may not include the part(s) on which the diagnostic characters can be found. Therefore, not only is it likely that some fossil species represented in the fossil record will go unrecognized, but the majority of fossil specimens lack species-diagnostic traits and therefore generally cannot be readily assigned to the species level based on apomorphy-based species diagnoses.

Nonetheless, despite the importance of fossil species and the importance of understanding the deficiencies of the fossil record when it comes to revealing species, paleotaxonomists generally publish their work without explicit reference to theoretical or operational species concepts, although it is readily apparent that the paleotaxonomic literature does not adhere to a consistent set of operational species criteria. Due to this lack of clarity, paleobiologists commonly substitute the genus for the species as the most easily recognizable and expedient taxonomic unit (Forey et al., 2004). Nonetheless, genera are higher taxa that theoretically, if not always in practice, represent monophyletic clusters of species ranging in numbers from one species to many and are not the most appropriate fundamental taxonomic unit for biostratigraphic, phylogenetic, paleoecological, and other evolutionary studies. Genera and other higher taxonomic ranks lack the potential for fundamental equivalence and although a total equivalence of modern and fossil species may ultimately never be achievable, morphologically delimited species are the best approximations of macroevolutionary units available in the fossil record.

The middle Eocene brontotheriid, *Metarhinus*, is a particularly good example of the importance and challenge of species

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taxonomy in paleontology. The genus itself is a highly recognizable small brontotheriid taxon, and species belonging to this genus share a distinctive set of diagnostic character states, including a highly specialized premaxillomaxillary rostrum, an elongate nasal incision, laterally protruding orbits, and a small infraorbital jugal process. Fossils of *Metarhinus* are abundant in deposits of early Uintan age (46.3–42.8 Ma) from the Western Interior of North America, including the Wagonhound Member of the Uinta Formation of Utah, the Adobe Town Member of the Washakie Formation of Wyoming, and to a lesser extent, the Sand Wash Basin of Moffat County, Colorado (Osborn, 1929; Turnbull and Martill, 1988; Mader, 1998; Mhlbachler, 2008). Although many species of *Metarhinus* from the Western Interior were named by early paleontologists, only two of these are valid and morphologically diagnosable species, *M. fluviatilis* Osborn (1908) and *M. abbotti* (Riggs, 1912) (see discussion in Mhlbachler, 2008). Deposits of early Uintan age in Southern California (Friars Formation and Member B of the Santiago Formation) are additional loci for fossils of *Metarhinus* (Walsh, 1996), including *M. pater* Stock (1937), endemic to Southern California. Much of the fossil material from these localities is relatively fragmentary, consisting of partial upper and lower dentitions and limb bones. However, more recent collections from Southern California include more diagnostic material (e.g., partial and/or nearly complete skulls) that preserves morphological features that offer more insights into *Metarhinus* taxonomy, diversity, and paleobiology.

Although there are distinct morphospecies within the genus *Metarhinus*, rigorous definition and differentiation of these taxa is rendered problematic due to the fragmentary nature of most fossil specimens (Mhlbachler, 2008). For example, the only consistent character that appears to distinguish *M. fluviatilis* from *M. abbotti* is a difference in the shape of the nasal bone. Only those few skulls in which a nasal bone is preserved can be identified to species, and these specimens do not show notable differentiation in other aspects of their morphology. For this reason, the vast majority of specimens attributed to the genus *Metarhinus* can be assigned to neither species due to lack of preservation of the diagnostic nasals. This situation renders it difficult, despite a wealth of *Metarhinus* fossils, to investigate aspects of variation within and between species.

The paleobiogeographic pattern for species of *Metarhinus* is also perplexing because there is a persistent tendency for these minimally differentiated sister taxa to occur in the same geologic formations. *Metarhinus fluviatilis* and *M. abbotti* coexist in the Wagonhound Member of the Uinta Formation; *Metarhinus fluviatilis* co-occurs with *M. pater* in the Friars formation; and the Santiago Formation includes *M. pater* and an additional species of *Metarhinus*, possibly *M. abbotti*. The consistent co-occurrences of *Metarhinus* sister taxa in both Southern California and the Western Interior suggests sympatric speciation, a controversial speciation pattern that has not been convincingly demonstrated to occur in Mammalia (Via, 2001; Coyne and Orr, 2004). Therefore, it seems questionable to conclude that *Metarhinus* morphospecies actually represent sympatric but reproductively distinct population units. Alternative hypotheses for the co-occurring *Metarhinus* morphotaxa, representing non-equivalence to modern species, would include sexual dimorphism and/or other sources of intraspecific variability such as ontogenetic change.

The goals of this investigation are to (1) revise the diagnosis and description of *Metarhinus pater* using previously unreported fossil material collected from the Friars and Santiago formations and investigate its phylogenetic position within the Brontotheriidae; (2) document the co-occurrence of other *Metarhinus* morphospecies in the same formations; (3) examine morphologic variation in the *Metarhinus* fossil material from Southern California and the Western Interior; and (4) consider the relevance

of these findings to the taxonomy, diversity, paleobiology, and biogeography of *Metarhinus*.

## STRATIGRAPHIC CONTEXT

The holotype maxilla/premaxilla of *Metarhinus pater* (LACM/CIT 2037) was collected from an interbedded sequence of fluvial sandstones and conglomerates (LACM/CIT locality 249) mapped by Hanna (1926) as part of the Poway Conglomerate (Stock, 1937). Later, Schiebout (1977) reassigned LACM/CIT locality 249 to the Friars Formation following the stratigraphic revisions of Kennedy and Moore (1971), Peterson and Kennedy (1974), Kennedy (1975), and Kennedy and Peterson (1975) in which the Poway Conglomerate was elevated to group status and subdivided into three formations, including from oldest to youngest, the Stadium Conglomerate, Mission Valley Formation, and Pomerado Conglomerate. For reasons that remain unclear these authors chose to include strata of the Friars Formation in the La Jolla Group (a stratigraphic sequence of marine shales, siltstones, and sandstones), rather than in the Poway Group, a sequence of fluvial mudstones, sandstones, and conglomerates with which the Friars Formation shares many lithostratigraphic and facies similarities.

Based on extensive field and laboratory work, Walsh (1996) and Walsh et al. (1996) provided a thorough redescription of the lithostratigraphy, biostratigraphy, magnetostratigraphy, and biochronology of the Friars Formation, subdividing the rock unit into three informal members, including a lower sandstone and mudstone tongue, a middle conglomerate tongue, and an upper sandstone and mudstone tongue. The type area for the Friars Formation occurs at the confluence of Mission Valley, Murphy Canyon, and Alvarado Canyon in the central part of metropolitan San Diego and includes the type locality of *Metarhinus pater* (LACM/CIT locality 249). Walsh (1996) noted that vertebrate fossils (primarily land mammals) recovered from the Friars Formation (undifferentiated strata in the type area, as well as strata in the lower, middle, and upper tongues) represented a distinct and homogeneous assemblage to which he applied the name 'Poway fauna.' Characteristic mammalian taxa in the Poway fauna include *Peratherium* sp. cf. *P. knighti* McGrew, 1959, *Aetomylus simplicidens* Novacek, 1976, *Scenopagus* sp. cf. *S. priscus* (Marsh, 1872), *Centetodon aztecus* Lillegraven et al., 1981, *Stockia powayensis* Gazin, 1958, *Microsypops kratos* Stock, 1938, *Uintasorex montezumicus* Lillegraven, 1976, *Hesperolemur actius* Gunnell, 1995, *Microparamys* sp. cf. *M. minutus* (Wilson, 1937), *Sciuravus powayensis* Wilson, 1940, *Metarhinus?* *pater* Stock, 1937, *Merycobunodon littoralis* Golz, 1976, and *Leptoreodon major* Golz, 1976.

Fossil specimens of *Metarhinus* are locally common in the Friars Formation and typically occur as isolated maxillae, dentaries, and teeth, often in fluvial channel sandstones. This is the case for the holotype of *M. pater* (LACM/CIT 2037), as well as for the majority of questionably referred specimens of cf. *Metarhinus* sp. Occasionally, more complete specimens are recovered from caliche-rich, overbank mudstone/siltstone strata. Included here is a nearly complete skull of *M. pater* (SDSNH 51340) and a partial skull of *M. fluviatilis* (SDSNH 112402).

As noted by Walsh (1996), the Poway Fauna contains taxa typically found in strata of early Uintan age (Uintan biochron U<sub>11</sub> of Robinson et al., 2004). Further, Walsh et al. (1996) emphasized that exposures of the middle conglomerate and upper sandstone and tongues of the Friars Formation in the northern portion of metropolitan San Diego had been erroneously mapped by Kennedy and Peterson (1975) as the younger Stadium Conglomerate and Mission Valley Formation, respectively. Recognition of these mapping errors clarified the lithostratigraphic relationships of the middle Eocene rock units in metropolitan San Diego

and resolved the disparity observed by Golz and Lillegraven (1977) and Novacek and Lillegraven (1979) concerning the distinctly different fossil mammal assemblages recovered from the southern and northern outcrops of sedimentary rocks mapped by Kennedy (1975) as the Mission Valley Formation. Walsh (1996) thus demonstrated that late Uintan land mammals occur in the southern sandstone outcrops of the true Mission Valley Formation, whereas early Uintan land mammals occur in northern sandstone outcrops mapped as the Mission Valley Formation, but actually belonging to the Friars Formation.

Magnetostratigraphic analyses of strata in and near the type area of the Friars Formation recognized a normal interval in the lower part of the section and a reversed interval in the upper part (Flynn, 1986; Walsh et al., 1996). These authors suggested correlation of this stratigraphic sequence with chrons C21n and C20r, respectively, thus indicating a geochronologic age of ~43.8 to 47.8 Ma for the Friars Formation.

Eocene sedimentary rocks exposed in northwestern San Diego County have also produced fossils referable to *Metarhinus pater* (Walsh, 1991, 1996); however, these strata lack the distinct deposits of Poway-type conglomerates upon which much of the stratigraphic subdivision of the La Jolla and Poway groups is based. Without these conglomerates and their obvious sequence stratigraphic implications, it is practically difficult to apply the San Diego stratigraphic nomenclature of Kennedy and Moore (1971) to the middle Eocene strata in this area. Instead, most workers assign these strata to the Santiago Formation of Woodring and Popenoe (1945), which was originally named for a sequence of Eocene marine siltstones and sandstones that crop out in the western foothills of the Santa Ana Mountains in Orange County, California. It was Wilson (1972) who first suggested that there were lithostratigraphic and biostratigraphic similarities between the type Santiago Formation in Orange County and middle Eocene marine and nonmarine strata in northwestern San Diego County. Further, Wilson (1972) subdivided the San Diego County strata of the Santiago Formation into three informal members: a basal marine member (Member A); a middle marine member (Member B); and a nonmarine upper member (Member C). In his summary of the Eocene mammalian biochronology of San Diego County, Walsh (1996) demonstrated that Wilson's (1972) Santiago Formation Member B is of early Uintan age, whereas Member C is of late Uintan and Duchesnean age. Age-diagnostic fossils have not yet been recovered from Member A. Characteristic mammalian taxa from Member B (Mesa Drive local fauna of Walsh, 1991, 1996) include *Peratherium* sp. cf. *P. knighti* McGrew, 1959, *Peradectes* sp., *Crypholestes vaughni* (Novacek, 1976), *Batodonoides powayensis* Novacek, 1976, *Washakius woodringi* (Stock, 1938), *Uintasorex montezumicus* Lillegraven, 1976, *Microparamys* sp. cf. *M. minutus* (Wilson, 1937), *Sciuravus powayensis* Wilson, 1940, and *Metarhinus? pater* Stock, 1937.

Fossil specimens of *Metarhinus* are locally common in Member B of the Santiago Formation and typically occur as isolated maxillae, dentaries, teeth, and limb bones, generally in estuarine and nearshore marine sandstones. This is the case for many of the questionably referred specimens of cf. *Metarhinus* sp. More complete specimens consisting of associated cranial and postcranial elements are rare, but have been recovered from estuarine shell beds of Member B. Examples include a partial skull of *M. pater* (SDSNH 98272) and a partial skeleton referred to cf. *Metarhinus* sp. (SDSNH 107852).

The Member B strata containing the Mesa Drive local fauna occur within a 7-m-thick sequence of interbedded estuarine sandstones, siltstones, and mudstones at the top of an 18-m-thick section (Mesa Drive stratigraphic section) that begins with open marine sandstones and siltstones (Walsh, 1996). An unconformity at the top of Member B is overlain by coarse-grained fluvial sandstones of Member C.

Magnetostratigraphic analysis of strata from the Mesa Drive stratigraphic section recognized a reversed interval in the Member B portion of the section and a normal interval in the Member C portion (Prothero, 2001). The Member B portion of the stratigraphic section was in turn correlated with Chron C20r, indicating a geochronologic age of ~43.8 to 46.2 Ma.

This lithostratigraphic and biostratigraphic summary indicates that all specimens of *Metarhinus* from San Diego County are derived from strata (Friars Formation and Member B of the Santiago Formation) deposited during the beginning of Uintan biochron U<sub>II</sub> of Robinson et al. (2004).

## MATERIALS AND METHODS

### Species Delimitation and Phylogenetic Analysis

The following revised diagnosis and description of *Metarhinus pater* and other *Metarhinus* taxa follow Mhlbachler (2008) in format and terminology. The methods of taxon delimitation employed here are derived from the phylogenetic species concept where species are partitioned into the smallest phenotypically (in this case, morphologically) diagnosable clusters of specimens (Cracraft, 1989; Nixon and Wheeler, 1990; Wheeler and Platnick, 2000), following operational guidelines detailed by Mhlbachler (2008). Character data for *M. pater* were derived from the three specimens that are referred to that species below and were added to the phylogenetic data matrix of Mhlbachler and Deméré (2009) using characters originally described in Mhlbachler (2008) (Supplementary Data, Tables 1S and 2S). For this analysis, an additional fifth character state ('posterior margin of nasal incision positioned above the posterior margin of M2') was added to multistate character 6. This character state differentiates *M. pater* from all other brontotheres, except *Embolotherium grangeri*, which shares with *M. pater* the same condition. Phylogenetic Analysis Using Parsimony (PAUP\* version 4.0b10) (Swofford, 2001) was used to find the most parsimonious trees using the heuristic search algorithm, imposing a monophyletic ingroup and paraphyletic outgroup. All multistate characters were ordered with the exception of character 26 and character 73. For the latter, a special character-state tree was constructed in MacClade (Maddison and Maddison 2005) (see Mhlbachler, 2008). Two of the four outgroup taxa are early hippomorph perissodactyls "*Hyracotherium*" (*Xenicohippus osborni* sensu Froehlich 2002) and *Pachynolophus*. Other outgroup taxa are *Lambdaotherium popoagicum* and *Dangania pingi*, an early Chinese perissodactyl. Both of these taxa are postulated to have been the sister taxon of Brontotheriidae (Mader, 1998; Beard, 1998; Hooker and Dashzeveg, 2003; Mhlbachler and Holbrook, 2008).

### Coefficient of Variation Analysis

The coefficient of variation (CV: defined as  $100 \times \text{standard deviation/mean}$ ), a size-independent statistical ratio of the mean and standard deviation (Sokal and Rohlf, 1995), is commonly used in mammalian paleontology to compare the extent of size variation among species, or, as used here, to test hypotheses about the number of species that constitute an osteological sample (Cope and Lacy, 1995; Carrasco 1998; Plavcan and Cope, 2001; Colbert, 2006). Mammal species tend to show restricted levels of size variation with CVs (usually less than or near a value of 10), with the exception of secondary sex traits such as horn length or tusk size, which, in sexually dimorphic species, can have values that are much higher than non-sexual traits (Mhlbachler et al., 2004; Mhlbachler, 2005, 2007a).

Coefficients of variation of *Metarhinus* assemblages, including material referred to species and undiagnostic material that has been referred to *Metarhinus* sp. and cf. *Metarhinus* sp. from the Friars, Santiago, Uinta, and Washakie formations (derived from

a subset of the data included in the supplemental material) are compared to two referents: (1) a monospecific mass death assemblage (MDA) of *Metarhinus* sp. from the Washakie Formation initially described by Turnbull and Martill (1988); and (2) a bulk sample of *Mesatirhinus junius*, a similarly sized Bridgerian-aged brontothere from the Bridger, Washakie, and Sand Wash formations. The *Metarhinus* MDA presumably represents a time-synchronous sample of individuals from a single population that lacks significant time- or space-averaging and represents the minimum expectation of variation within this species. The *Mesatirhinus junius* sample, on the other hand, is a time- and space-averaged bulk sample of all specimens attributable to that species regardless of locality or stratigraphic plane and represents a sample in which intraspecific variation might exceed that of a time-synchronous population sample because it includes regional variation in addition to possible anagenetic fluctuation in size (e.g., Muhlbachler et al., 2002).

*Metarhinus* morphologic data from the Friars, Santiago, Washakie, and Uinta formations are summarized in Tables 1–4. Data for referents (*Mesatirhinus junius* and *Metarhinus* sp. MDA) are reported in Muhlbachler (2008). Assuming that the Friars, Santiago, Uinta, and (probably) Washakie samples of *Metarhinus* are mixtures of two or more distinct morphotypes, the objective of this analysis is to test the null hypothesis that the degree of size variation in these samples does not exceed the degree of variation for a single species. Exceptionally high coefficients of variation in comparison to the referents would falsify the null hypothesis of a single species and indicate that the assemblages are composed of a mixture of species with different mean sizes.

**Institutional Abbreviations**—AMNH, American Museum of Natural History, New York; CMNH, Carnegie Museum of Natural History, Pittsburgh; FMNH, Field Museum of Natural History, Chicago; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LACM/CIT, California Institute of Technology collection now in the Natural History Museum of Los Angeles County, Los Angeles; SDSNH, San Diego Natural History Museum, San Diego; UCM, Museum of Natural History, University of Colorado; UCMP, Museum of Paleontology, University of California at Berkeley.

**Anatomical Abbreviations**—alc, anterolingual cingular cusp; CL, maximum diameter of upper canine crown; cL, maximum diameter of lower canine crown; cmf, central molar fossa; eam, external auditory pseudomeatus; fl, foramen lacerum; fo, foramen ovale; if, infraorbital foramen; ip, infraorbital process; M1–M3,

TABLE 1. Summary statistics for selected morphometric variables of *Metarhinus fluviatilis*, *Metarhinus pater*, and *Metarhinus* sp. from the Friars Formation.

	N	Mean	SD	Min	Max	CV
CL	3	19.8	1.36	18.2	20.1	6.90
P3L	5	18.1	2.38	15.7	21.6	13.13
P3W	5	21.4	1.29	20.0	22.6	6.03
M2L	7	35.5	4.22	30.2	40.6	11.89
M2W	7	35.4	3.47	29.5	38.6	9.82
P2–P4	3	52.9	4.77	47.4	55.8	9.01
M1–M3	3	100.8	11.69	87.8	110.4	11.59
VL	1	487.0	—	—	—	—
cL	1	18.1	—	—	—	—
p3L	7	18.2	1.40	15.6	19.5	7.69
p3W	5	12.4	0.85	11.3	13.5	6.83
m2L	6	32.0	1.68	30.0	34.6	5.25
m2W	7	19.6	1.02	18.3	20.8	5.20
p2–p4	3	55.8	1.36	54.6	57.3	2.44
m1–m3	3	104.3	4.10	101.2	109.0	3.93

**Abbreviations:** CV, coefficient of variation; **Max**, maximum; **Min**, minimum; **N**, number of specimens; **SD**, standard deviation.

TABLE 2. Summary statistics for selected morphometric variables of *Metarhinus abbotti* and *Metarhinus* sp. from the Santiago Formation, Member B.

	N	Mean	SD	Min	Max	CV
CL	2	16.9	2.17	15.4	18.5	12.83
P3L	8	17.5	2.14	14.3	20.1	12.21
P3W	8	20.4	1.25	18.9	22.2	6.14
M2L	6	36.7	0.91	35.6	37.6	2.47
M2W	6	35.5	1.52	34.2	38.1	4.27
P2–P4	5	52.6	2.46	49.4	54.8	4.68
M1–M3	2	96.9	3.43	94.5	99.4	3.54
p3L	7	18.3	1.10	17.0	19.8	6.04
p3W	8	12.1	1.07	10.5	13.9	8.85
m2L	7	31.4	2.22	28.2	34.0	7.05
m2W	7	18.6	1.49	16.3	20.3	8.03
p2–p4	3	56.5	2.34	54.0	58.7	4.15
m1–m3	3	106.1	9.50	96.0	114.9	8.95

Abbreviations: as in Table 1.

anteroposterior length of upper molar row; **m1–m3**, anteroposterior length of lower molar row; **M2**, second upper molar; **M2L**, anteroposterior length of upper second molar; **m2L**, anteroposterior length of lower second molar; **M2W**, buccolingual width of upper second molar; **m2W**, buccolingual width of lower second molar; **M3**, third upper molar; **o**, orbit; **P2–P4**, anteroposterior length of upper second, third, and fourth premolars; **p2–p4**, anteroposterior length of lower second, third, and fourth premolars; **P3L**, anteroposterior length of upper third premolar; **p3L**, anteroposterior length of lower third premolar; **P3W**, buccolingual width of upper third premolar; **p3W**, buccolingual width of lower third premolar; **pn**, posterior nares; **VL**, total length of skull measured on the ventral surface.

## SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1785

Order PERISSODACTYLA Owen, 1848

Family BRONTOTHERIIDAE Marsh, 1873

Subfamily BRONTOTHERIINAE Marsh, 1873

*METARHINUS PATER* Stock, 1937

**Holotype**—LACM/CIT 2037, a right maxilla with C–M3.

**Type Locality**—LACM/CIT locality 249, Friars Formation, undifferentiated (previously referred to as the Poway conglomerate), San Diego County, California, U.S.A. “Sandstones of the Poway formation, exposed on the west bank of the San Diego

TABLE 3. Summary statistics for selected morphometric variables for *Metarhinus fluviatilis*, *Metarhinus abbotti*, and *Metarhinus* sp. from the Wagonhound member of the Uinta Formation.

	N	Mean	SD	Min	Max	CV
CL	9	17.1	1.5	14.8	19.4	9.0
P3L	14	18.3	1.7	14.8	21.3	9.2
P3W	13	21.9	1.4	19.7	24.3	6.4
M2L	11	36.7	2.4	33.8	41.4	6.6
M2W	12	36.7	3.1	32.8	43.1	8.5
P2–P4	13	53.0	3.5	47.8	60.1	6.6
M1–M3	12	96.2	6.0	87.0	103.6	6.2
p3L	15	17.7	1.9	14.5	21.5	10.9
p3W	13	13.1	1.3	10.9	14.7	10.2
m2L	16	33.2	2.6	30.0	38.4	7.9
m2W	13	19.8	2.0	17.0	22.7	10.0
p2–p4	13	54.8	4.8	46.0	64.5	8.7
m1–m3	15	104.0	7.7	92.9	119.3	7.4

Abbreviations: as in Table 1.

TABLE 4. Summary statistics for selected morphometric variables for *Metarhinus fluviatilis*, and *Metarhinus* sp. from the Adobe Town Member of the Washakie Formation (excluding specimens from the *Metarhinus* sp. MDA).

	N	Mean	SD	Min	Max	CV
CL	2	16.7	2.2	15.1	18.2	13.1
P3L	12	18.4	1.7	15.3	20.5	9.1
P3W	11	21.8	1.3	19.4	24.6	5.9
M2L	8	37.6	1.7	35.4	39.9	4.4
M2W	10	35.9	1.4	32.9	37.7	4.0
P2–P4	9	53.9	2.6	50.3	59.0	4.9
M1–M3	6	99.1	3.9	93.1	103.9	3.9
p3L	8	18.8	2.7	14.3	22.5	14.6
p3W	7	13.9	2.5	8.8	16.7	17.8
m2L	6	35.7	2.6	33.0	40.0	7.2
m2W	6	23.0	3.0	18.7	27.5	12.9
p2–p4	8	58.9	5.8	48.1	67.8	9.9
m1–m3	7	112.1	7.7	107.0	128.9	6.8

Abbreviations: As in Table 1.

River, approximately one-quarter mile north and east of the Mission San Diego.” (Stock, 1937:49).

**Age**—Middle Eocene (early Uintan NALMA).

**Referred Specimens**—(SDSNH locality 3833, Mission Terrace, Friars Formation, undifferentiated, San Diego County, California, U.S.A.) SDSNH 51340, partial skull with right I3, P1–P4, M3, left I3, P2–P3, M3, and additional isolated elements, including three incisors, two canines, right M1, M2, left P4, M2, and a number of vertebrae; (SDSNH locality 4566, Santiago Formation, Member B, Oceanside, San Diego County, California, U.S.A.) SDSNH 98272, partial skull with right C, P3–M3, left P4–M3 (all partial). One additional specimen, SDSNH 50472, a nasal bone from SDSNH locality 3788 (Friars Formation, San Diego County, California, U.S.A.), probably belongs to *M. pater*.

**Diagnosis**—*Metarhinus pater* is a relatively small brontothere with a nasal incision that extends to a point posterodorsal to the anterior margin of the M2. The nasal process tapers distally in

width, is dorsoventrally thin, horizontally oriented, unelevated, with very shallow lateral walls. The orbits strongly protrude laterally and are positioned above the posterior portion of the M2 and anterior portion of the M3. The premaxillomaxillary rostral cavity is enclosed by bone dorsally and its dorsal surface is nearly horizontal. Other cranial characteristics include a small infraorbital process, strongly curved and unbowed zygomatic arches, and a ventrally open and mediolaterally angled external auditory pseudomeatus. Ventral sphenoidal fossae are absent. Dentally, *M. pater* is characterized by large subcaniniform upper incisors, a simple P1, a distinct P2 metacone, weak premolar preprotocristae on P2 and P3, and with short lingual crests occasionally extending posteriorly from the premolar protocones. Premolar hypocones are absent. The molars of *M. pater* have tall, lingually angled ectoloph with weak labial ribs, and thinned lingual ectoloph enamel with wedge-shaped paracones and metacones. Central molar fossae and anterolingual circular cusps are present (although it is possible that these were absent in some individuals). Cingular parastyle shelves, paraconules, and metoloph are absent.

*Metarhinus pater* shares with *M. fluviatilis* and *M. abbotti* a specialized rostrum that is sealed dorsally by bone, laterally protruding orbits, and a small infraorbital process. *Metarhinus pater* differs from *M. fluviatilis* by its distally tapered nasal and differs from all other species of *Metarhinus* by its anteroposteriorly longer nasal incision.

## Description

**Skull**—The holotype of *Metarhinus pater* (LACM/CIT 2037) is a skull fragment consisting of a right maxilla and premaxilla with canine and complete cheektooth row (Fig. 1). Additional specimens referable to this species are SDSNH 51340, a skull missing its dorsal surface with heavily worn dentition (Figs. 2 and 3), and SDSNH 98272, a poorly preserved anterior half of a skull with right canine and incomplete cheektooth row (Fig. 4). Finally, an isolated nasal bone (SDSNH 50472) likely represents *M. pater* (Fig. 5). The few specimens referable to *M. pater* suggest a species

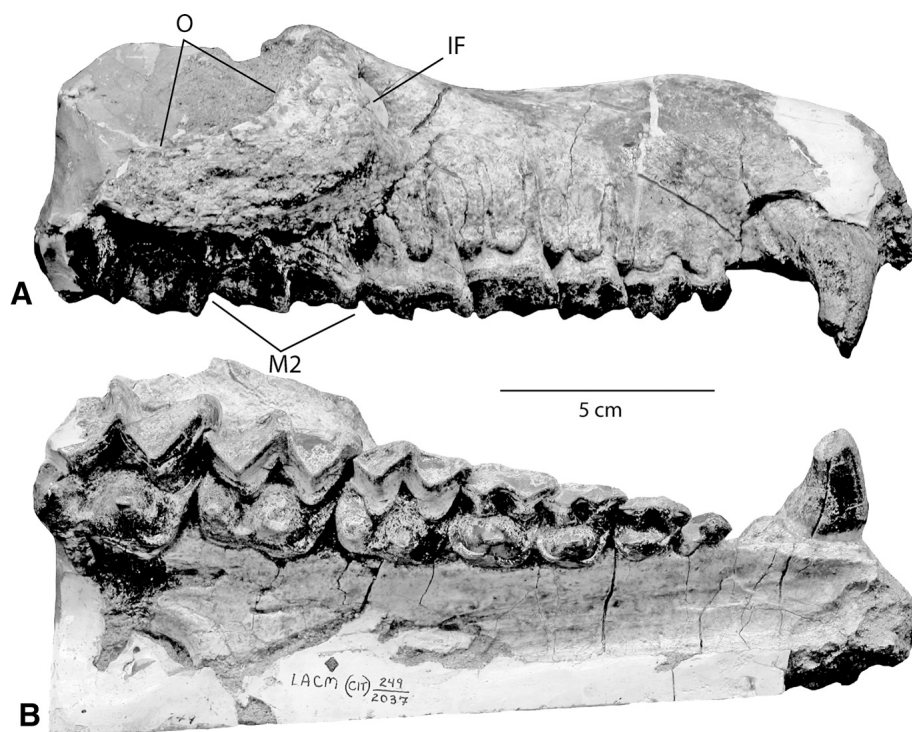


FIGURE 1. The holotype skull fragment of *Metarhinus pater* (LACM/CIT 2037) from the Friars Formation. **A**, Right view; **B**, ventral view with left upper tooth row.

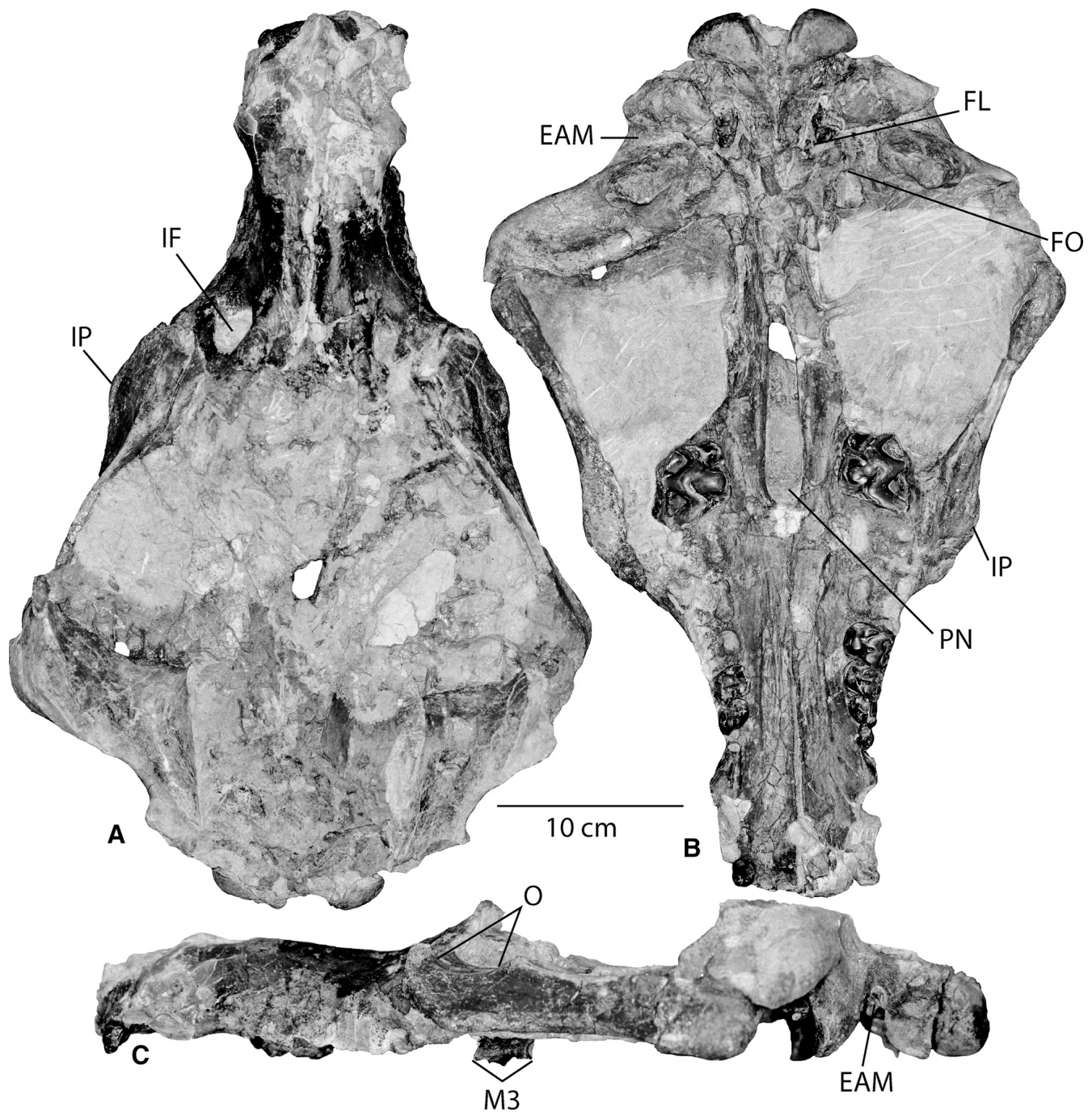


FIGURE 2. Ventral portion of a partial skull (SDSNH 51340) from the Friars Formation referred to *Metarhinus pater*. **A**, view of dorsal weathered surface; **B**, ventral view; **C**, left view.

that is slightly larger than *M. fluviatilis* and more similar in size to *M. abbotti* (Fig. 6A).

SDSNH 98272 is the only specimen with a preserved frontonasal region. There are no bony protuberances (or horns) of any sort on this specimen. No skull sutures are visible on this specimen. The rostrum of *Metarhinus pater* is highly derived in the same manner as *Dolichorhinus hyognathus* (Osborn, 1889), *M. fluviatilis*, and *M. abbotti* where the dorsal surface of the rostrum is enclosed in bone, except at the midline where there is an open groove where the cartilaginous nasal septum would have in-

serted. In most other respects, the premaxillomaxillary rostrum resembles that of *M. fluviatilis* and *M. abbotti*. From the lateral view, the premaxillomaxillary rostrum is long, slightly upturned, and of relatively constant thickness throughout its length. Despite these similarities, the rostrum of *M. pater* appears to be more elongate than other species of the same genus, due to the longer nasal incision. This difference is apparent in all three of the partial skulls that are referred to *M. pater*. In the holotype specimen (LACM/CIT 2037) the dorsal surface of the rostrum is nearly horizontal throughout most of its length. Moving



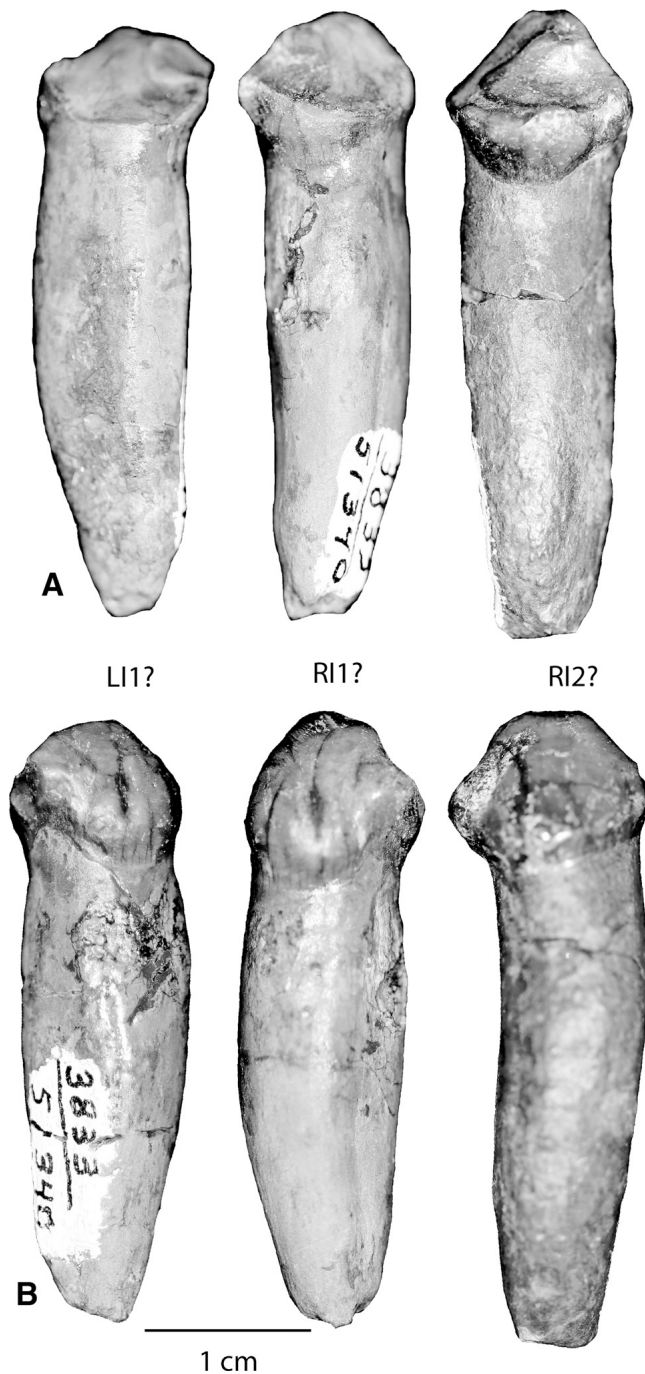


FIGURE 3. Upper incisors associated with *Metarhinus pater* skull from the Friars Formation (SDSNH 51340). **A**, lingual views; **B**, labial views.

posteriorly, it begins to slope shallowly in a posterodorsal direction just above the M1. The nasal incision of this specimen was anteroposteriorly very long and would have extended posteriorly at least to a point above the mesostyle of the M2. The incomplete nasal incision of SDSNH 51340 extended at least to the posterior margin of M2. Only one specimen (SDSNH 98272) provides a complete nasal incision. Its nasal incision is consistent with the type specimen in its length and is also dorsoventrally quite deep, with its dorsal margin positioned higher than the orbit.

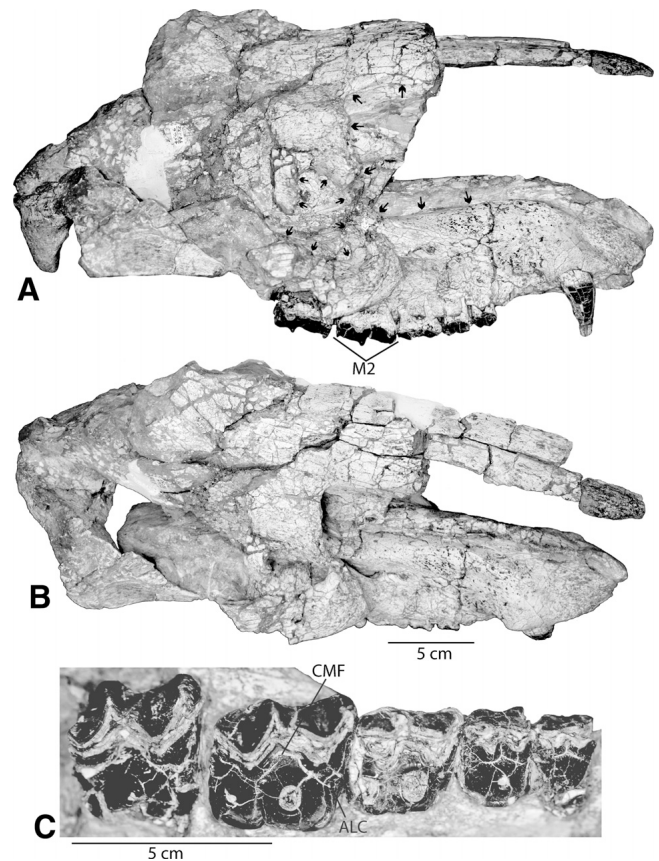


FIGURE 4. Partial skull (SDSNH 98272) from Member B of the Santiago Formation referred to *Metarhinus pater*. **A**, right view; **B**, right view rotated slightly to show dorsal surface; **C**, right P3–M3. Black arrows trace the outline of the orbit and nasal incision.

The anteroposterior length of the nasal incision in *Metarhinus pater* is rivaled only by *Embolotherium grangeri*, a large-bodied late Eocene Central Asian brontothere where the nasal incision (obviously derived independently of *M. pater*) extended

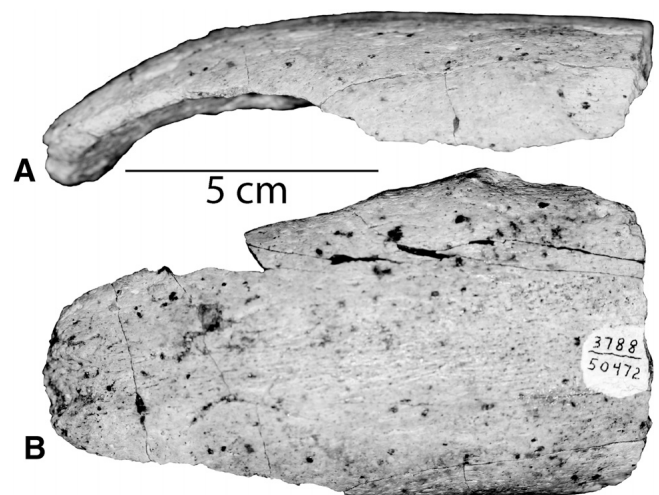


FIGURE 5. Probable nasal (SDSNH 50472) of *Metarhinus pater* from Member B of the Santiago Formation. **A**, left view; **B**, dorsal view.



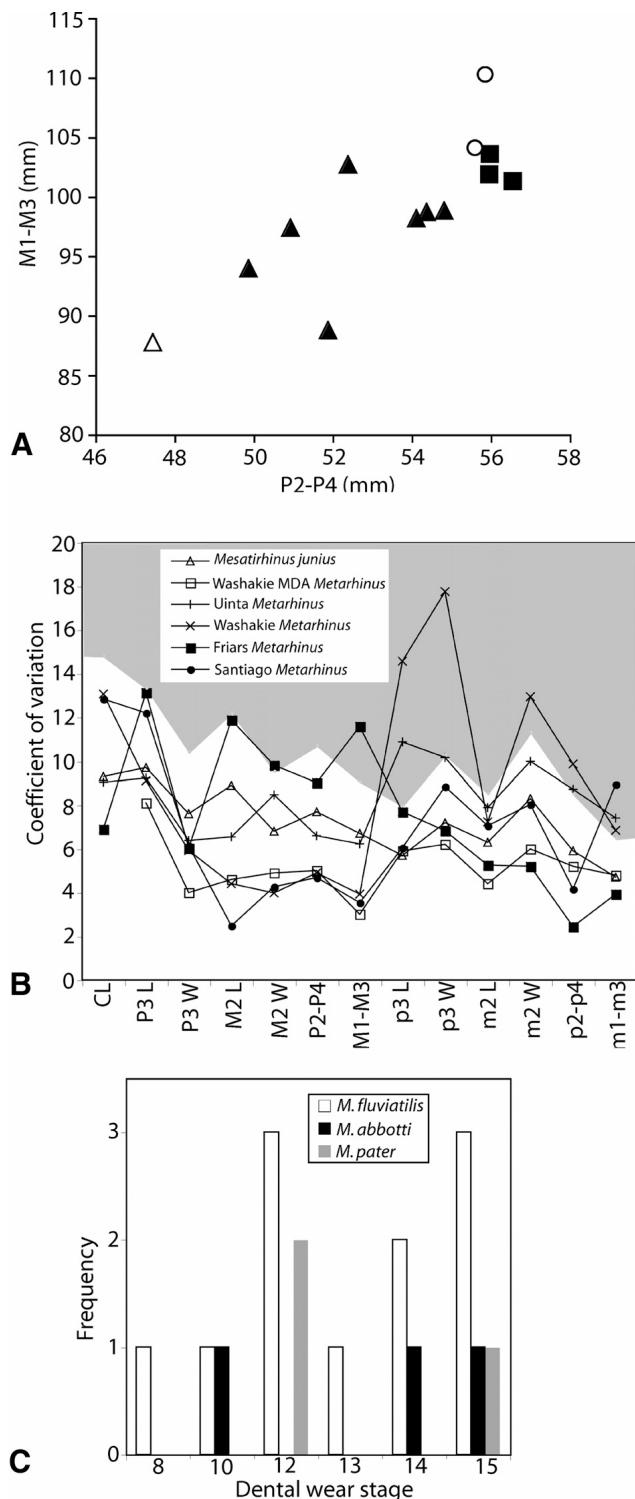


FIGURE 6. Variation analysis of *Metarhinus* assemblages. **A**, upper dental tooth row data (mm) for the species of *Metarhinus*. **Symbols**: △, *Metarhinus fluviatilis* from the Friars Formation; ▲, *Metarhinus fluviatilis* from the Uinta and Washakie Formations; ■, *Metarhinus abbotti* from the Uinta Formation; ○, *Metarhinus pater* from the Friars Formation. **B**, coefficients of variation for selected dental measurements from *Metarhinus* from the Friars formation and the Santiago Formation, compared to coefficients of variation for a mass death assemblage population sample of *Metarhinus* sp. from the Washakie Formation (Mihlbachler, 2008) and a referent species, *Mesatirhinus junius*, with shaded region indicating values above the upper 95% confidence limit for the CVs of *Mesatirhinus junius*; **C**, histogram depicting the ontogenetic age distributions of specimens attributable to *Metarhinus fluviatilis*, *M. abbotti*, and *M. pater* based on brontothere upper dental wear stages described by Osborn (1929).

to a point above the M2. Although the faces of *M. fluviatilis* and *M. abbotti* are highly constricted by the nasal incision, it is not to the same degree as *M. pater*. In *M. fluviatilis* and *M. abbotti* the posterodorsal surface of the rostrum slopes much more steeply upward (dorsally) and the nasal incision extends no farther posteriorly than the anterior margin of the M2.

Related to the fact that the nasal incision of *Metarhinus pater* is longer, the orbit and infraorbital foramen are also positioned more posteriorly in comparison to *M. fluviatilis* and *M. abbotti*. In all three skulls of *M. pater*, the orbit is positioned above the posterior portion of M2 and the anterior portion of M3, with the anterior-most margin of the orbital rim above the posterolateral root of M1. Likewise, the infraorbital foramen pierces the skull above the posterolateral root of the M1. The orbits of *M. fluviatilis* and *M. abbotti* are consistently positioned above the M2 and are entirely anterior to the M3, with the anterior-most border of the orbital rim above the anterolateral root of M1. Likewise, the infraorbital foramina of *M. fluviatilis* and *M. abbotti* are above the anterolateral root of M1.

Although the right edge of the nasal bone of SDSNH 98272 is broken, the right distal end is intact. On the left side the distal end is missing but the left edge of the proximal two thirds of the nasal process is intact. The remaining portions of the nasal process indicate a narrow nasal bone with roughly parallel lateral margins and a slightly tapered (in dorsal aspect) distal margin. The nasal process of *Metarhinus pater* differs markedly from that of *M. fluviatilis* where the nasal process is strongly flared distally, but it is not different from the thin, distally tapered nasal process of *M. abbotti*. However, in skulls of *M. abbotti*, the nasal process tends to be shorter than the premaxillomaxillary rostrum, whereas in the skull of *M. pater* the nasal process and rostrum are of equal length. Another specimen (SDSNH 50472) from Member B of the Santiago Formation, a more finely preserved distal end of a nasal process, possibly belongs to *M. pater* (Fig. 5). At the proximal end of the nasal fragment the lateral walls are shallow with thin and roughened edges. The lateral walls do not extend to the distal half of the fragment, where the nasal bone strongly arches ventrally. From a dorsal view, the lateral edges of the proximal (posterior) end of the nasal fragment are parallel, whereas the distal end tapers and terminates in a rounded roughened distal margin. The nasal fragment (SDSNH 50472) in particular resembles the nasal process of CMNH 2866, a skull of *M. abbotti* from the Uinta Formation. Presumably this fragment represents *M. pater* because this taxon is known to be present from the Santiago Formation. However, because *M. pater* and *M. abbotti* have similar nasals, we cannot rule out the possibility that the nasal fragment is not *M. abbotti*.

Other aspects of the skull of *M. pater* are not unlike *M. fluviatilis* or *M. abbotti*. SDSNH 51340 preserves the complete ventral portion of a skull (Fig. 2). From a lateral view, the jugal portion of the zygomatic arch is dorsoventrally shallow and horizontal, whereas the squamosal portion of the zygomatic arch is deeper and rises abruptly posteriorly. From dorsal and ventral views, the zygomatic arches have an angular appearance. The jugal extends posterolaterally and there is a nearly 90° bend in the arch at the jugal-squamosal junction. A small infraorbital process is found on the jugal. A similar process is not apparent on LACM/CIT 2037 (the holotype) or SDSNH 98272, although that portion of the jugal appears to have been abraded in the former and broken in the latter. The infraorbital process of the jugal is much smaller than those of *Dolichorhinus hyognathus*, *Sphenocoelus uintensis*, and *Mesatirhinus junius*, but is similar to other species of *Metarhinus*. Another small flange can be seen more posteriorly, along the ventral margin of the jugal below its junction with the squamosal on SDSNH 51340. A similar structure is seen on skulls of *M. fluviatilis*.

The anterior rim of the posterior nares of SDSNH 51340 is slightly anterior to the M3 protocones, whereas in the holotype (LACM/CIT 2037) it is just slightly anterior to the M3 protocones. A narrow horseshoe-shaped rim emarginates the

anterior and lateral margins of the posterior nares. Many species of brontotheres, including *M. fluviatilis*, show evidence of having turbinates extending posteriorly from the posterior nares (Mihlbachler, 2008). No evidence for posteriorly extended turbinates is seen in *M. pater*, but this easily could be an artifact of nonpreservation of the fragile turbinates. The posterior nares form an elongate canal, a typical brontothere character, that tends to extend onto the anterior part of the sphenoid. Enlarged ventral sphenoidal fossae, like those seen in *Sphenocoelus uintensis*, are absent in *M. pater*. The external auditory pseudomeatus enters the skull in an almost completely mediolateral direction. The occipital condyles are normally proportioned, unlike the enlarged condyles of *Dolichorhinus hyognathus* and *Sphenocoelus uintensis*. Like most other hornless brontotheres, the mastoid process does not contact the postglenoid process ventrally; therefore, the external auditory pseudomeatus is open ventrally. The remaining aspects of the basicranium of SDSNH 51340 are unremarkable with typical brontothere traits, such as widely separated foramen ovale and foramen lacerum.

**Upper Dentition**—The upper incisors of the holotype specimen are not preserved; however, SDSNH 51340 includes a pair of lateral incisors (I3s) in situ and three heavily worn isolated large upper incisors that represent elements of the upper incisor row (Fig. 3). The incisor alveoli and/or partial roots of this specimen indicate an unreduced number of incisors (three pairs) that form an arched row anterior to the canines. The in situ third incisors and the least extensively worn of the three isolated specimens (probably an I2) have a subcaniniform crown morphology with prominent lingual cingula. The remaining incisors associated with SDSNH 51340 are more extensively worn but appear to have had a similarly shaped crown. The incisors of *Metarhinus pater* are not different from those of *M. abbotti*. The upper incisors of *M. fluviatilis* are only partially known, although it is likely that this species had similar incisors (Mihlbachler, 2008; also see description of *M. fluviatilis* below).

All three specimens of *M. pater* have canines that are relatively large but within the normal range of variation seen among brontotheres. (Those of SDSNH 51340 are isolated and not figured.) The canines of brontotheres tend to vary in size more so than other teeth, possibly due to sexual dimorphism, and it is possible that the canines of these specimens do not reveal the total range of canine size variation for the species to which they belong (i.e., the specimens may belong to the same sex). A short postcanine diastema is present in all three specimens.

The holotype specimen (LACM/CIT 2037) includes a complete right upper cheektooth row and is the primary basis for the following description. The cheekteeth of SDSNH 51340 and SDSNH 98272 are more worn and fragmented.

The P1 crown is a small tooth with a single cusp and a heavily worn posterior heel. There is no evidence of a diastema between P1 and P2.

The P2 is has a slightly more oblique outline than P3 and P4 due to a more posterolingually angled anterior margin. The parastyle of P2 bends just slightly anterolingually. The parastyle of P3 is straight, whereas that of P4 is angled anterolabially. The metastyle of P2 is essentially straight, whereas the P3 and P4 metastyles are angled posterolabially. The labial walls of P2–P4 have distinct labial paracone ribs that become less distinct on more posterior premolars. The labial metacone ribs are more diminished than the labial paracone ribs. There is only a single large lingual cusp (protocone) on P2–P4. A short lingual crest extends posteriorly from the P2 protocone and descends the posterior slope of this cusp. A similar crest is seen on P3 and P4, but on these teeth the lingual crest is very short, giving the protocones of these teeth an oval appearance. On P2 there is a faint hint of a preprotocrista but the more posterior premolars lack evidence of this structure. The anterior and posterior cingula of the P3 and P4 are much more prominent than the cingula of P2.

On all three of these premolars the cingula are not connected on the lingual side of the crown; however, like many other species of Brontotheriidae, this final trait varies intraspecifically. The P4 of SDSNH 98272 shows a continuous lingual cingulum.

The upper molars of *Metarhinus pater* show a number of apomorphies not unlike the molars of *M. fluviatilis* and *M. abbotti*. The molar ectolophs are lingually angled and taller than the lingual cusps. The vertical labial ribs on the paracone and metacone are weak. In molars that show minimal wear, such as the M3 of LACM/CIT 2037 (Fig. 1B), the lingual sides of the paracone and metacone are wedge-shaped and the enamel on the lingual side of the ectoloph is thinner overall than the enamel of the labial side of the ectoloph. In molars that are more heavily worn, such as the M1 and M2 of LACM/CIT 2037, the lingual ectoloph enamel is more extensively worn, revealing that the lingual sides of the paracone and metacone are more rounded at their proximal bases and the enamel is somewhat thickened. The pattern of variation in enamel thickness and cusp shape is typical of all brontotheres except the most basal members, such as *Eotitanops* and *Palaeosyops*. The anterior molar cingulum does not climb to the peak of the parastyle to form a small shelf. Instead, the anterior molar cingula pass proximally to the distal peak of the parastyle.

Like other species of *Metarhinus*, each molar of *M. pater* has a shallow central fossa situated within the trigon (between the margins of the protocone, paracone, and metacone). There is a distinct swelling (anterolingual cingular cusp) on the anterior cingulum of each molar just anterior to the protocone. This cingular cusp is also apparent on the molars of SDSNH 98272. There are no traces of paraconules or metalophs. The M3 of LACM/CIT 2037 has a prominent hypocone slightly smaller than the hypocones of M1 and M2. The labial molar cingula are thin but distinct and discontinuous around the lingual bases of the mesostyles; lingual molar cingula are faint and discontinuous.

#### *METARHINUS FLUVIATILIS* Osborn, 1908a

**Neotype**—FMNH P12187, a complete skull missing only the incisors.

**Type Locality**—Wagonhound Member (Uinta B) of the Uinta Formation, Uinta Basin, Utah, U.S.A.

**Age**—Middle Eocene (early Uintan NALMA).

**Synonyms**—*Metarhinus riparius* Riggs, 1912.

**Referred Specimens**—(SDSNH locality 5717, Friars Formation, upper tongue, San Diego County, California, U.S.A.) SDSNH 112402, skull with right I3–C, P2–M3, left P2–M3. See Mihlbachler (2008) for specimens referred to *Metarhinus fluviatilis* from the Wagonhound Member of the Uinta Formation of Utah and the Adobe Town Member of the Washakie Formation of Wyoming.

**Diagnosis**—see Mihlbachler (2008).

#### Description

One skull (SDSNH 112402) from the Friars Formation can be identified as *Metarhinus fluviatilis* (Fig. 7). SDSNH 112402 is somewhat smaller than skulls identified as *M. fluviatilis* from the Uinta and Washakie formations (Fig. 6A). *Metarhinus fluviatilis* was recently redescribed by Mihlbachler (2008); therefore a full diagnosis and description are not given here. Only details pertaining to the specific identification of SDSNH 112402 are described below.

The skull is nearly complete but lacking some of its anterior dentition. It has been plastically deformed so that the dorsal portion of the skull is artificially shifted posteriorly. The relatively small size, highly derived elongate premaxillomaxillary rostrum, anteroposteriorly elongate nasal incision, small infraorbital flanges, and laterally protruding orbits are characteristic of the genus *Metarhinus*.

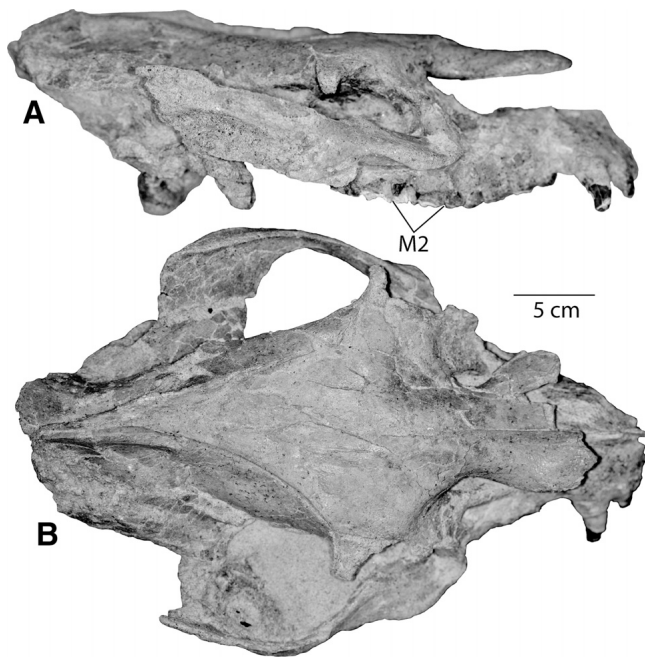


FIGURE 7. Skull (SDSNH 112402) from the Friars Formation referred to *Metarhinus fluviatilis*. **A**, right view; **B**, dorsal view showing distally flared nasal.

In terms of its specific identification, this skull is distinct from specimens referred to *M. pater* and *M. abbotti*. The dorsal surface of the rostrum is flat from its anterior end to a point above the anterolateral root of the M1. Posterior to this point it angles sharply posterodorsally. This aspect of the shape of the rostrum closely resembles *M. fluviatilis* and *M. abbotti* and differs from *M. pater*. In *M. pater*, the flat dorsal surface of the rostrum continues to a point above the anterolateral root of the M2 where it then rises posterodorsally at a much shallower angle. The nasal incision of SDSNH 112402 extends to a point above the mesostyle of the M2; however, this is largely an artifact of the posterior displacement of the dorsal surface of the skull. Likewise, the ovalized orbits and strong angle of the occiput are artificial.

The left nasal process of SDSNH 112402 is badly damaged, and the anterior edge of the right side is incomplete. However, the right side is sufficiently complete to show that the nasal process of SDSNH 112402 is narrower than the rostrum, mediolaterally constricted proximally, but much broader distally. The shape of the nasal bone clearly indicates affinity with *M. fluviatilis*. Both *M. abbotti* and *M. pater* have distally tapered nasal bones, whereas *M. fluviatilis* has a distally broadened nasal bone identical to that of SDSNH 112402, with shallow lateral walls, a thin distal margin, and an overall width that is narrower than the width of the rostrum.

The dentition of SDSNH 112402 is heavily worn, but does not contradict other species of *Metarhinus*. However, incisors are not preserved on any other specimen referable to *M. fluviatilis*. The preserved right I3 of SDSNH 112402 is worn and slightly damaged, but suggests a similar subcaniniform incisor morphology known in other *Metarhinus* species.

cf. *METARHINUS* sp.

**Referred Specimens from the Friars Formation, San Diego County, California, U.S.A.**—(LACM/CIT locality 249-S, Friars Formation, undifferentiated) LACM 55550, right m1 or m2;

LACM 56125, right M1 or M2; (LACM locality 3243, Friars Formation, undifferentiated) LACM 56253, left m1 or m2; (SDSNH locality 3612, Friars Formation, upper tongue) SDSNH 47840, skull fragments with right I1–I3, C, P1, ectolophs of P4–M3, and numerous partial postcranial elements, including innominate, scapula, sacrum, and vertebral fragments; (SDSNH locality 3621, Friars Formation, conglomerate tongue) SDSNH 55877, left M (partial); SDSNH 55878, left m3; SDSNH 55879, right dentary fragment with ?dp2; SDSNH 55880, right P2; SDSNH 55881, left dp4; SDSNH 55882, left dp3; SDSNH 55883, left P4; SDSNH 55884, right M2 fragment; SDSNH 55885, canine; SDSNH 55886, incisor; SDSNH 58650, lower premolar fragment; (SDSNH locality 3623, Friars Formation, upper tongue) SDSNH 43269, right P4; SDSNH 43274, left P2–M1; SDSNH 43275, partial mandible with right p4 (partial), m1–m2, m3 (partial); (SDSNH locality 3637, Friars Formation, undifferentiated) SDSNH 42873, right m3; SDSNH 78853, left m1; (SDSNH locality 3639, Friars Formation, undifferentiated) SDSNH 78878, symphysis with partial left and right canines; (SDSNH locality 3655, Friars Formation, lower tongue) SDSNH 46221, mandible with right p2–m3, left p2–m3; (SDSNH locality 3681, Friars Formation, upper tongue) SDSNH 46585, right maxilla fragment with M2–M3; SDSNH 47365, edentulous left mandible fragment; (SDSNH locality 3784, Friars Formation, undifferentiated) SDSNH 49605, left maxilla with M3; SDSNH 50564, right dentary fragment with m3; SDSNH 50600, left dentary with dp2–dp4; (SDSNH locality 3788, Friars Formation, undifferentiated) SDSNH 49557, left M; SDSNH 49562, canine; SDSNH 49564, left M; SDSNH 49578, right M3; SDSNH 50570, mandibular symphysis with right and left i1, c; SDSNH 50592 right dentary fragment with p3–p4; (SDSNH locality 4698, Friars Formation, upper tongue) SDSNH 84412, mandible with right p3–m3, left p4–m3, partial humerus; (SDSNH locality 4959, Friars Formation, upper tongue) SDSNH 91696, mandible with right and left p1–m3; (UCMP locality V6888, Friars Formation, undifferentiated) UCMP 113184, partial mandibular symphysis; UCMP 113201, a partial mandible with right dp3–dp4, and m1; UCMP 113203, a mandible fragment with left m3; UCMP 113194, a mandible fragment with right m2; (UCMP locality V6889, Friars Formation, undifferentiated) UCMP 95774, a right maxilla with M1–M3; UCMP 95780, a partial mandible with left m1–m3; (UCMP locality V 68156, Friars Formation, undifferentiated) UCMP 95808, a right maxilla with dp4 and M1; UCMP 95809, a left maxilla fragment with P3–P4; UCMP 95813, a partial mandible with right m2 (partial), and m3; UCMP 113189, a right p2; (UCMP locality V 68157, Friars Formation, undifferentiated) UCMP 95831, a left M1 or M2; (UCMP locality V 68160) UCMP 95841, a mandible fragment with right p2–p3; (UCMP locality V 72158, Friars Formation, upper tongue) UCMP 113182, fragments of a skull, jaw, and some isolated lower teeth; UCMP 113199 left M1 or M2; (UCMP locality V 72176, Friars Formation, upper tongue) UCMP 106011, right p3, p4, and m1.

**Referred Specimens from the Santiago Formation, Member B, San Diego County, California, U.S.A.**—(SDSNH locality 3486) SDSNH 38347, maxilla fragment with P2–P3, P4 (partial); SDSNH 38348, right maxilla fragment with P1–P3; SDSNH 38349, right M2 or M3; SDSNH 38350, left maxilla with C–P4; SDSNH 38366, mandibular ramus with p2–m2; SDSNH 38367, left mandibular ramus with p3–p4; SDSNH 38368, left m2; SDSNH 38369, right p1–3; SDSNH 38370, edentulous mandibular symphysis; SDSNH 38371, left mandibular ramus with p3–m1, m2–m3 (partial); SDSNH 38372, right mandibular ramus with p3–m3; SDSNH 38373, right maxilla fragment with M1–M2, M3 (partial); SDSNH 38374, left maxilla with P2–M2; SDSNH 38375, partial left mandibular ramus with m2–m3 (partial); SDSNH 38376, right M2–M3; SDSNH 38377, left maxilla fragment with P2–P3; SDSNH 38378, right maxilla with M1–M3; SDSNH 38379, left maxilla with P2–M1; SDSNH 38380, right mandibular ramus with

p2–m2; SDSNH 38381, left p3–p4, m1–m3; SDSNH 38382, right p4–m3; SDSNH 38383, left ramus with p3–m3; SDSNH 83847, left m3; (SDSNH locality 4566) SDSNH 98273, right dentary with p4–m3, and postcranial fragments including thoracic vertebrae, ribs, and a tibia; SDSNH 107852, juvenile mandibular ramus with left dp4; (SDSNH locality 5487) SDSNH 105842, right maxilla with P1–M2, M3 (partial), and left maxilla fragment with P2–P4 (broken); SDSNH 105843, partial mandible with canine roots, right p1, p2 (broken), p3–m3, and left p3–m1 (broken).

### Description

Fossil specimens of *Metarhinus* lacking the nasal bone and/or diagnostic aspects of the rostrum cannot readily be assigned to species and are therefore here referred to cf. *Metarhinus* sp. The large collections of *Metarhinus*-sized brontothere material from the Friars and Santiago formations probably represent a mixture of species. Some of these specimens possess unusual characteristics that differ from known specimens of *M. fluviatilis*, *M. abbotti*, and/or *M. pater*. These differences include occasional additional cusps on upper premolars, the absence of anterolingual cingular cusps and central molar fossae on the upper molars, and lower premolars with unusually elongate proportions. These anomalies could represent variations among *M. pater* or other species of *Metarhinus* from Southern California or they could represent a brontothere other than *Metarhinus*, although the later hypothesis seems less likely because no diagnostic fossils indicating a brontothere other than *Metarhinus* are yet known from these deposits.

**Friars Formation**—*Metarhinus fluviatilis* and *M. pater* are known to occur in the Friars Formation and the remaining brontotheriid material from the Friars Formation likely represents a mixture of these two species, although we cannot rule out the presence of *M. abbotti* or other similarly sized brontotheres. Generally, the material here attributed to cf. *Metarhinus* sp. is consistent in size and morphology with *Metarhinus*, although several specimens show anomalous characteristics that could represent either intraspecific variations that occur among local *Metarhinus* populations or completely different species. For instance, SDSNH 43269, a *Metarhinus*-sized upper premolar (P4), has a tiny paracone. Other specimens (e.g., SDSNH 43274) show an occasional premolar hypocone, although they are absent on most specimens and when present are situated close to the protocone and strongly connected to it. Neither of these structures has been observed in the premolars of *Metarhinus* from the Uinta and Washakie formations, although they have been found to be intraspecifically variable in many other brontothere species (see distribution of phylogenetic character 53, state 2, in Table 1S) and do not necessarily indicate unique species. Many of the brontothere upper molars from the Friars Formation also deviate from typical *Metarhinus* morphology. The upper molars of all three *Metarhinus* species are characterized by a prominent anterolingual cingular cusp (a cusp-like peak on the anterior cingulum, anterior to the protocone) and a shallow central molar fossa (a depression in the enamel in the center of the crown). Many of the specimens of cf. *Metarhinus* sp. (SDSNH 46585, UCMP 95774) bear these traits, but in others (e.g., UCMP 95831, LACM 56125) these traits are absent or exceedingly weak. At least one other species of brontothere, *Sphenocoelus uintensis* Osborn (1895), is known to have a central molar fossa that is both present and absent (Mihlbachler, 2008), and it is possible that the same variations seen here are intraspecific and do not necessarily indicate the presence of additional species other than those already documented from the Friars Formation.

Among the mandibles of cf. *Metarhinus* sp. from the Friars Formation, there is variation in the position of the posterior margin

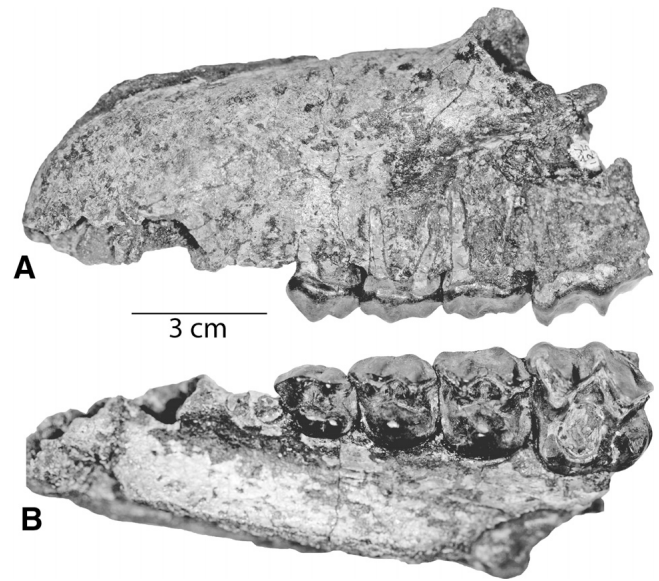


FIGURE 8. A left rostral fragment with P2–M1 (SDSNH 38379) from Member B of the Santiago Formation that does not belong to *Metarhinus pater* but possibly represents *M. fluviatilis* or *M. abbotti*. **A**, left view; **B**, ventral view showing occlusal surfaces of dentition.

of the symphysis, ranging from a position slightly anterior to the anterior margin of the p3 (SDSNH 43275) to near the posterior margin of the p3 (SDSNH 78878). This degree of variation resembles *Metarhinus* sp. jaws from the Uinta and Washakie formations (Mihlbachler, 2008).

**Santiago Formation**—*Metarhinus pater* is the only brontotheriid positively identified from Member B of the Santiago Formation, although certain brontotheriid specimens recovered from this formation indicate that at least one other species of *Metarhinus* is present. The most diagnostic of these is SDSNH 38379, a left premaxillomaxillary rostrum with P2–M1 (Fig. 8). The size and specialized morphology of this rostral fragment suggests a taxon unquestionably different from *M. pater*. The dorsal margin of the maxilla is flat distally, but begins to slope steeply posterodorsally at a point directly above the anterolateral root of the P4. Unfortunately, very little of the skull is preserved posterior to this point. However, the transition in the angle of the dorsal surface of the rostrum at this point is too abrupt for *M. pater* and bears a distinct resemblance to *M. fluviatilis* and *M. abbotti*.

Like the material from the Friars Formation, specimens of cf. *Metarhinus* sp. from the Santiago Formation show a similar array of peculiarities not entirely consistent with any known species of *Metarhinus*. These peculiarities include occasional (but very rare) hypocones on P2 (SDSNH 39379) and the absence of anterolingual cingular cusps and central molar fossae on the upper molars (e.g., SDSNH 38374). Metaconids are variably present (SDSNH 38367) and absent (SDSNH 38366) on the p3, although this trait is also found to be variable among *Metarhinus* sp. from the Uinta and Washakie formations. More significantly, the lower premolars of numerous specimens of cf. *Metarhinus* sp. from the Santiago Formation appear to be buccolingually narrower than those of other species of *Metarhinus*, including cf. *Metarhinus* sp. from the Friars Formation. As noted above, the significance of these variations is uncertain; they are likely to represent local variations in *Metarhinus* populations but could represent entirely new taxa.

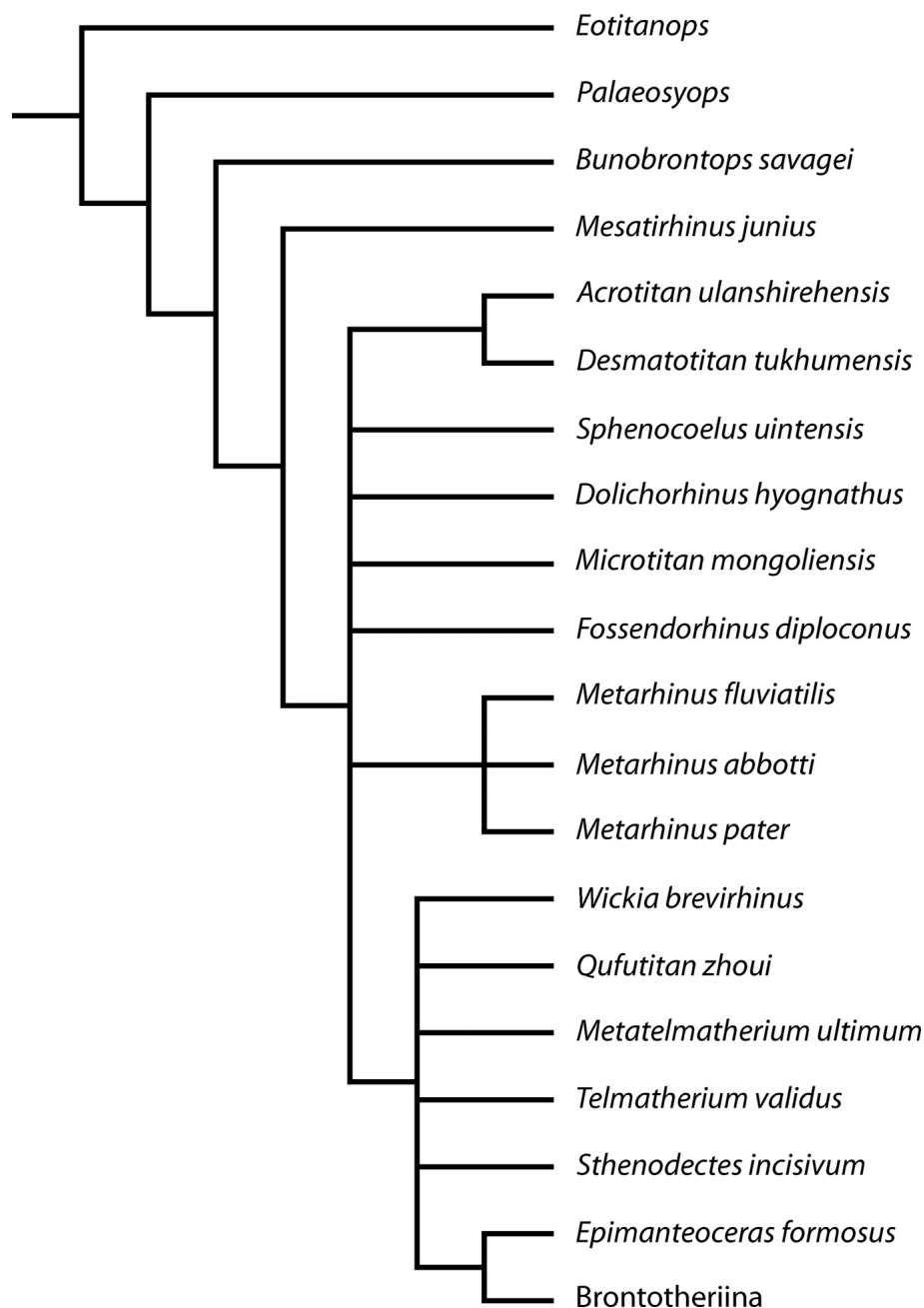


FIGURE 9. Reduced strict consensus phylogeny of Brontotheriidae, with *Nanotitanops shanghuangensis* removed a posteriori, showing the phylogenetic position of *Metarhinus pater*. For simplicity, Brontotheriina, the monophyletic subtribe of brontotheres that possess conspicuous frontonasal protuberances (horns), representing 28 species included in the heuristic search, is shown here as a single branch.

## RESULTS

### Phylogenetic Analysis

Phylogenetic analysis yielded 535978 most parsimonious trees with lengths of 315 steps. Like earlier analyses of brontothere phylogeny (Mihlbachler, 2007b, 2008; Mihlbachler and Deméré, 2009), the excessive number of trees is largely due to one taxon (*Nanotitanops shanghuangensis*) whose phylogenetic position is highly unstable. A posteriori removal of this taxon yields the reduced strict consensus tree in Figure 9. The introduction of *Metarhinus pater* and modification of character 6 (as explained in Materials and Methods) did not yield results that conflict with the most recent phylogenetic analysis (Mihlbachler and Deméré, 2009); therefore we present only a brief summary of the results here, highlighting the phylogenetic position of *M. pa-*

*ter* and the status of the genus *Metarhinus*. Although the portion of the cladogram in which *Metarhinus* resides is poorly resolved, *Metarhinus* is monophyletic with no phylogenetic resolution within the genus. An apomorphy-based diagnosis of the genus *Metarhinus* involves the following conditions: (character 6) nasal extending to the posterior margin of M1 or more posterior; (character 14) orbits protruding prominently laterally; (character 17) premaxillomaxillary rostrum sealed dorsally by a bony cover; (character 68) and large anterolingual cingular cusp on the upper molars (Mihlbachler, 2008).

### Coefficient of Variation Analysis

Figure 6a is a plot of upper tooththrow dimensions of *Metarhinus* skulls from Southern California and Western Interior localities

that are each identifiable as one of the three species. This graph suggests that *M. pater* and *M. abbotti* are of similar size and that both are larger than *M. fluviatilis*. The single *M. fluviatilis* skull from the Friars Formation is the smallest specimen attributable to a species of *Metarhinus*, whereas specimens attributed to *M. pater* are among the largest. These apparent size differences suggest that *M. fluviatilis* can be differentiated from other species on the basis of size. However, the samples of diagnostic *M. pater* and *M. abbotti* skulls are too small to understand the total range of size variation within these species and to what degree they overlap with *M. fluviatilis* and each other.

Results of the CV analysis, which includes both species-diagnostic specimens and the additional specimens of cf. *Metarhinus* sp., are plotted in Figure 6B, with the shaded region indicating values above the upper 95% confidence limit for the CVs of *Mesatirhinus junius*. The differences in CV values between the time- and space-averaged *Mesatirhinus junius* sample and the *Metarhinus* sp. MDA are as predicted, with CVs generally being higher for the former, due to time- and space-averaging. The *Metarhinus* samples from the Uinta, Washakie, Friars, and Santiago formations are probably time-averaged to some extent. The Washakie Formation *Metarhinus* sample (excluding the Washakie MDA) yields the highest CVs. Five traits, all from the lower dentition, have CVs above the 95% confidence limit of *Mesatirhinus junius*. In contrast, the upper dental variables from the Washakie *Metarhinus* assemblage are lower and similar in magnitude to the MDA. The CVs of the Uinta sample do not reach the extreme values seen in the Washakie sample; however, the Uinta *Metarhinus* assemblage shows a similar pattern, with lower CVs among the upper dental variables. The CVs for the Uinta upper dental variables resemble the *Mesatirhinus* referent in magnitude, whereas the lower dental variables are generally higher, with four variables at or above the upper 95% confidence limit of the *Mesatirhinus junius* sample. The overall pattern of variation in the Santiago sample resembles the Uinta and Washakie samples in that the upper dental traits yield considerably lower CVs than the lower dental traits. Overall, however, the Santiago sample has CVs that are similar in value to the referent samples, with no variables yielding CVs above the 95% confidence limit of *Mesatirhinus junius*. The Friars *Metarhinus* assemblage shows a contrasting pattern of variation, with higher CVs among the upper dental variables. Four upper dental traits have CVs that are at or above the upper 95% confidence interval of the *Mesatirhinus junius* sample. The CVs of the lower dental traits from the Friars sample are all considerably lower, with three of the six variables yielding lower CVs than any other sample.

## DISCUSSION

### Taxonomic Status of *Metarhinus pater*

Stock (1937) erected "*Metarhinus* (?)" *pater* on a right maxilla with upper canine and cheekteeth. This species was differentiated from Uinta Basin representatives of *Metarhinus* (known at the time) based on the "great backward extension of the nasomaxillary notch. . ." "The ascent of the lower border of the notch in its posterior course is more gradual than in skulls of (other *Metarhinus* species) . . . and extends behind the level of the antorbital foramen. . ." (Stock, 1937:49). Stock's observations on the type specimen are accurate and differentiate it, despite its incomplete condition, from *M. fluviatilis* and *M. abbotti*. Subsequently, *M. pater* was considered a possible synonym of *M. diploconus* and *M. abbotti* (Mader, 1998; 2008). Mhlbachler (2008) found *M. fluviatilis*, *M. abbotti*, and *M. diploconus* to be distinct species and assigned the latter to a new genus, *Fossendorhinus*, based largely on differences in its premaxillomaxillary rostrum and internal nasal morphology. Mader (2008; 2009a) has rejected the genus *Fossendorhinus*, along with nearly all other taxonomic revisions and phylogenetic results of Mhlbachler (Mader, 2008,

2009a, 2009b) and suggests that the distinctive morphology of *F. diploconus* is a result of individual variation, although it is unclear how Mader derived this interpretation. One of us (MM) has examined the same specimens and the primary differences between the two species (*F. diploconus* and *M. abbotti*) as described by both Mhlbachler (2008) and noted by Mader (2009a) do not appear to be consistent with common patterns of intraspecific variation found in other species of Brontotheriidae (Mhlbachler, 2007b; 2008; Mhlbachler et al., 2004). Moreover, the differences are sufficient to force *Fossendorhinus* outside of the genus *Metarhinus* altogether in phylogenetic analyses of Brontotheriidae (Mhlbachler, 2008; Mhlbachler and Deméré, 2009, this paper).

Therefore, in addition to *M. pater*, the two additional species of *Metarhinus* are *M. fluviatilis* and *M. abbotti*. *Metarhinus pater* clearly possesses morphological features that are characteristic of *Metarhinus*. Mhlbachler (2008) concluded that the type specimen of *M. pater* represented an unknown species belonging to the genus *Metarhinus*, but considered this species a *nomen dubium* because, (1) there is some fluctuation in exact shape and length of the nasal incisions of both *M. fluviatilis* and *M. abbotti*, and (2) it was not known whether the outlying shape and length of the holotype of *M. pater* was anomalous or a consistent species-level difference. The discovery of additional specimens from both the Friars Formation and the Santiago Formation with elongate rostra and deeper nasal incisions confirms the presence of a morphotype that is distinct from *M. fluviatilis* and *M. abbotti*, thus validating the species *M. pater*. These additional specimens of *M. pater* also reveal a distally tapered nasal bone, which further differentiates *M. pater* from *M. fluviatilis*. Inclusion of *M. pater* in a phylogenetic analysis of the Brontotheriidae (Fig. 9) confirms that *M. pater* is a third member of the genus *Metarhinus*.

### Significance of *Metarhinus* Species

The three *Metarhinus* species recognized here are readily diagnosed by unambiguous differences: one has a distally flared nasal bone (*M. fluviatilis*), one has a distally tapered nasal bone (*M. abbotti*), and the third species has a distally tapered nasal bone and an unusually long nasal incision (*M. pater*). Other than the diagnostic aspects of nasal bone and rostrum, there are apparently no other differences in the dentitions and crania that can be used to readily differentiate these species. Moreover, it is observed that *Metarhinus* always occurs in species pairs; *Metarhinus fluviatilis* and *M. abbotti* are found in the same levels of the Uinta Formation, whereas *M. fluviatilis* and *M. pater* co-occur in the Friars Formation. In the Santiago Formation, *M. pater* co-occurs with a currently unknown *Metarhinus* species that could be *M. fluviatilis* or *M. abbotti*.

The persistent co-occurrences of these species pairs indicate their populations extensively overlapped geographically in a relatively narrow window of geologic time and were possibly sympatric. Unlike modern species, population processes, including those that play a role in speciation, such as gene flow, are not observable in fossil species. Nonetheless, it would be desirable to have some sense that, within a given time slice, paleospecies are similar to modern species in the sense that their morphological distinctions arose and were maintained by either reproductive isolation or minimal hybridization. This raises the question as to whether the three *Metarhinus* morphotaxa actually represent distinct evolutionary units, or if they represent some other aspect of variation, such as intraspecific sexual dimorphism or ontogenetic stages.

Figure 6C shows the ontogenetic age distribution of skulls referred to the three *Metarhinus* morphospecies, using successive dental wear stages for brontotheriids defined by Osborn (1929:455). *M. fluviatilis*, the species represented by the most specimens, includes individuals ranging from subadults with



unerupted third molars (stage 8) to senescent individuals with maximally worn dentitions (stage 15). The few specimens belonging to other species extensively overlap the age range represented by the *M. fluviatilis* skulls. Thus, the observed differences in skull morphology do not appear to be attributable to ontogenetic age.

Higher levels of variation in horn size, horn shape, zygomatic arch thickness, and canine size are common patterns of intraspecific variation, probably representing sexual dimorphism, within the Brontotheriidae (Mihlbachler, 2008; Mihlbachler et al., 2004). However, no other hornless brontothere species are characterized by intraspecifically bimodal nasal bones. If the *Metarhinus* morphotaxa represent sexual variants instead, it would seem likely that variation in cranial size would be found to correlate with nasal bone shape. However, this does not appear to be the case. The fact that the smaller morphotype (*M. fluviatilis*) has the wider, larger nasal bones is also inconsistent with typical patterns of sexual dimorphism in Mammalia, where the larger sex (males), typically also has the larger and more elaborate secondary sex characters. Moreover, the co-occurrence of *M. fluviatilis* and *M. abbotti* in the Wagonhound Member of the Uinta Formation, and the co-occurrence of *M. fluviatilis* with a different morphotype, *M. pater*, in the Friars Formation, is obviously not a case of sexual dimorphism. If the differences were attributable to sexual dimorphism within a single species, the same combination of morphotypes would consistently co-occur.

Body size differences are among the most common differences of closely related species, at least in terms of mean values (e.g., mass and length), even if there is some overlap between species. Mihlbachler (2008) suggested the size differences between *M. fluviatilis* and *M. abbotti* from Western Interior localities were minimal and that more fragmentary *Metarhinus* specimens (lacking the species-diagnostic nasal bone) could not be assigned to species on the basis of size. Moreover, many of the non-diagnostic specimens identified as cf. *Metarhinus* sp. that must belong to either of these species are intermediate in size between the Southern California *M. fluviatilis* skull and the *M. pater* skulls plotted in Figure 6A. Therefore, although these species may have different mean sizes, it seems probable that there would have been some degree of overlap. Size does not appear to be a valid means for assigning specimens to *M. fluviatilis*, *M. abbotti*, or *M. pater*.

Overall, the levels of size variation in three out of the four potentially species-mixed *Metarhinus* samples (from the Uinta, Washakie, and Friars formations) slightly exceed the expected levels of variation for a monospecific assemblage even when time-averaging is taken into account. This finding provides weak support for the conclusion that these assemblages represent mixtures of two or more species of different mean size. The only species-diagnostic skulls in the Washakie *Metarhinus* sample belong to *M. fluviatilis*. However, the degree of size variation in the Washakie sample suggests that an additional species is represented, at least among the unidentified mandibles included with that assemblage. Specimens identifiable as both *M. fluviatilis* and *M. abbotti* are present in the Uinta sample. Although the levels of size variation in that assemblage are not particularly high, a few variables exceed expectations for a monospecific assemblage. Likewise, the Friars sample, which contains a mixture of specimens that can be identified as *M. fluviatilis* and *M. pater*, shows an extent of size variation in several variables that exceeds expectations for a single species. The variables among the Washakie, Uinta, and Friars samples showing the highest levels of variation are predominantly cheektooth dimensions. Although canines and anterior dentitions are commonly intraspecifically dimorphic among mammal species, cheektooth size dimorphism is not prevalent within Mammalia. Therefore, sexual dimorphism is an unlikely explanation for the high levels of variation in these variables. Speciation rather than intraspecific variation still seems to be the best explanation for the three *Metarhinus* morphotypes.

The Santiago *Metarhinus* assemblage contradicts the other samples in that the degree of variation found in the sample is more consistent with a single species. However, this assemblage is possibly a mixture of two species of similar mean size. This assemblage includes specimens attributable to *M. pater*, and another morphotype that is consistent morphologically with *M. fluviatilis* and *M. abbotti*. Given the lower levels of size variation in this assemblage, it seems more probable that the second morphotype in this assemblage represents *M. abbotti*, because the few skulls identified as *M. abbotti* are similar in size to those of *M. pater* (Fig. 6A).

The co-occurrences of *Metarhinus* species in Southern California and Western Interior localities suggests (1) that non-geographic reproductive barriers may have evolved between species with extensive range overlaps, and (2) that there might have been sufficient ecological differences between the species for their coexistence. Although little else can be done to further test reproductive barriers between *Metarhinus* species, paleoecological techniques such as dental microwear or stable isotope analysis represent means to further test hypotheses about paleoecology-speciation dynamics of *Metarhinus*.

The sympatric distribution pattern of *Metarhinus* species contrasts with the more general phylogeography of brontotheriids that suggest the majority of speciation in this family was allopatric. For instance, current hypotheses of brontothere phylogeny imply numerous (7–12) intercontinental dispersals of brontotheres between North America and Asia in the middle Eocene (Mihlbachler, 2008). The pattern of frequent transcontinental dispersal and subsequent back-dispersal that is implicit in brontotheriid phylogeny suggests that allopatric lineage splitting caused by long-range dispersal was the predominant mode of species diversification in the Brontotheriidae. In contrast, the paleobiogeography of *Metarhinus* is consistent with sympatric speciation (Dieckmann et al., 2004), a speciation pattern that not pervasive among mammals (Coyne and Orr, 2004).

However, it is not possible to rule out allopatric speciation within *Metarhinus* without better data, particularly from Asia. *Metarhinus* has not been positively identified in Asia; however, a few fragmentary dental specimens from the middle Eocene Irindmanhan Asian land mammal age fissure fills in the Jiangsu Province of Eastern China could represent an Asian form of *Metarhinus*. These specimens, originally attributed to *Microtitan* sp. by Qi and Beard (1996), were referred to cf. *Metarhinus* sp. by Mihlbachler (2008). The specimens (IVPP V11016, a lower molar; IVPP V11017, a partial upper molar) are inconsistent with all other small brontotheres known from Asia but are similar in size and morphology to North American *Metarhinus*. If these specimens do represent *Metarhinus*, it suggests that one or more of the North American *Metarhinus* species could be products of allopatric speciation, resulting from long-range dispersal of a lineage to Asia, followed by subsequent back-dispersal to North America of a lineage descended from the Asian branch. Improvements in our knowledge of Asian brontotheres from middle Eocene could potentially falsify sympatric speciation within *Metarhinus*.

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## LITERATURE CITED

- Barton, N. H. 2001. Speciation. *Trends in Ecology and Evolution* 16:325.
- Beard, K. C. 1998. East of Eden: Asia as an important center of taxonomic origination in mammalian evolution; pp. 5–39 in K. C. Beard and M. R. Dawson (eds.), *Dawn of the Age of Mammals in Asia*. Bulletin of the Carnegie Museum of Natural History 34.
- Benton, M. J., and P. N. Pearson. 2001. Speciation in the fossil record. *Trends in Ecology and Evolution* 16:405–411.
- Bock, W. J. 2006. Species concepts versus species categories versus species taxa. *Acta Zoologica Sinica* 52:421–424.
- Bruner, E. 2004. Evolution, actuality and species concept: a need for a palaeontological tool. *Human Evolution* 19:93–112.
- Carrasco, M. A. 1998. Variation and its implications in a population of *Cupidinimus* (Heteromyidae) from Hepburn's Mesa, Montana. *Journal of Vertebrate Paleontology* 18:391–402.
- Claridge, M. F., H. A. Dawah, and M. R. Wilson (eds.). 1997. *Species: The Units of Biodiversity*. Chapman and Hall, New York, 439 pp.
- Colbert, M. W. 2006. Variation and species recognition in Eocene tapirs from Southern California. *Journal of Vertebrate Paleontology* 26:712–719.
- Cope, D. A., and M. G. Lacy. 1995. Comparative application of the coefficient of variation and range-based statistics for assessing the taxonomic composition of fossil samples. *Journal of Human Evolution* 29:549–576.
- Coyne, J. A., and H. A. Orr. 2004. *Speciation*. Sinauer Associates, Sunderland, Massachusetts, 545 pp.
- Cracraft, J. 1989. Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation; pp. 28–59 in D. Otte and J. A. Endler (eds.), *Speciation and Its Consequences*. Sinauer, Sunderland, Massachusetts.
- Dieckmann, U., M. Doebeli, J. A. J. Metz, and D. Tautz. 2004. *Adaptive Speciation*. Cambridge University Press, Cambridge, U.K., 460 pp.
- Flynn, J. J. 1986. Correlation and geochronology of middle Eocene strata from the western United States. *Palaeogeography, Palaeoclimatology, Palaeoecology* 55:335–406.
- Forey, P. L., R. A. Fortey, P. Kenrick, and A. B. Smith. 2004. Taxonomy and fossils: a critical appraisal. *Philosophical Transactions of the Royal Society of London B* 359:639–653.
- Froehlich, D. J. 2002. Quo vadis eohippus? The systematics and taxonomy of the early Eocene equids (Perissodactyla). *Zoological Journal of the Linnean Society* 134:141–256.
- Golz, D. J., and J. A. Lillegraven. 1977. Summary of known occurrences of terrestrial vertebrates from Eocene strata of southern California. University of Wyoming, Contributions to Geology 15:43–65.
- Gould, S. J. 2002. *The Structure of Evolutionary Theory*. Harvard University Press, Cambridge, Massachusetts, 1433 pp.
- Hanna, M. A. 1926. *Geology of the La Jolla quadrangle, California*. University of California Publications in Geological Sciences 16: 187–246.
- Hooker, J. J., and D. Dashzeveg. 2003. Evidence for direct mammalian faunal interchange between Europe and Asia near the Paleocene-Eocene boundary; pp. 479–500 in S. L. Wing, P. D. Gingerich, B. Schmitz, and E. Thomas (eds.), *Causes and Consequences of Globally Warm Climates in the Early Paleogene*. Special Paper of the Geological Society of America 369.
- Horvath, C. D. 1997. Discussion: phylogenetic species concept: pluralism, monism, and history. *Biology and Philosophy* 12:225–232.
- Kennedy, M. P. 1975. *Geology of the San Diego metropolitan area, California. Section A, Western San Diego metropolitan area*. California Division of Mines and Geology, Bulletin 200:9–39.
- Kennedy, M. P., and G. W. Moore. 1971. Stratigraphic relations of upper Cretaceous and Eocene formations, San Diego coastal area, California. *American Association of Petroleum Geologists, Bulletin* 55:709–722.
- Kennedy, M. P., and G. L. Peterson. 1975. *Geology of the San Diego metropolitan area, California. Section B, Eastern San Diego metropolitan area*. California Division of Mines and Geology, Bulletin 200:45–56.
- Kimbel, W. H., and L. B. Martin (eds.). 1993. *Species, Species Concepts, and Primate Evolution*. Plenum Press, New York.
- Mader, B. J. 1998. Brontotheriidae; pp. 525–536 in C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), *Evolution of Tertiary Mammals of North America. Volume I: Terrestrial Carnivores, Ungulates, and Ungulate-like Mammals*. Cambridge University Press, Cambridge, U.K.
- Mader, B. J. 2008. A species level revision of Bridgerian and Uintan brontotheres (Mammalia, Perissodactyla) exclusive of *Palaeosyops*. *Zootaxa* 1837:1–85.
- Mader, B. J. 2009a. The cranial anatomy of *Metarhinus* (Mammalia, Perissodactyla, Brontotheriidae). *Journal of Vertebrate Paleontology* 29:1300–1305.
- Mader, B. J. 2009b. Details of the cranial anatomy of a primitive diplacodont brontothere, cf. *Protitanotherium*, from the Wiggins Formation of Wyoming (Mammalia, Perissodactyla, Brontotheriidae). *Journal of Vertebrate Paleontology* 29:1224–1232.
- Maddison, W. P., and D. R. Maddison. 2005. *MacClade 4.08: Analysis of Phylogeny and Character Evolution*. Sinauer Associates, Sunderland, Massachusetts.
- Mihlbachler, M. C. 2005. Linking sexual dimorphism and sociality in rhinoceroses: insights from *Teleoceras proterum* and *Aphelops malacothrinus* from the late Miocene of Florida; pp. 495–520 in R. C. Hulbert, Jr., G. S. Morgan, and J. A. Baskin (eds.), *Cenozoic Vertebrates of the Americas: Papers to Honor S. David Webb*. Bulletin of the Florida Museum of Natural History 45.
- Mihlbachler, M. C. 2007a. Sexual dimorphism and mortality bias in a small Miocene North American Rhino, *Menoceras arikarensis*: insights into the coevolution of sexual dimorphism and sociality in rhinos. *Journal of Mammalian Evolution* 14:217–238.
- Mihlbachler, M. C. 2007b. *Eubrontotherium clarnoensis*, a new genus and species of brontothere (Brontotheriidae, Perissodactyla) from the Hancock Quarry, Clarno Formation, Wheeler County, Oregon. *Paleobios* 21:19–39.
- Mihlbachler, M. C. 2008. Species taxonomy, phylogeny, and biogeography of the Brontotheriidae (Mammalia: Perissodactyla). *Bulletin of The American Museum of Natural History* 311:1–475.
- Mihlbachler, M. C., C. A. Hemmings, and S. D. Webb. 2002. Morphological chronoclines among late Pleistocene Muskrats (*Ondatra zibethicus*: Muridae, Rodentia) from Northern Florida. *Quaternary Research* 58:289–295.
- Mihlbachler, M. C., S. G. Lucas, and R. J. Emry. 2004. The holotype specimen of *Menodus giganteus*, and the “insoluble” problem of Chadronian brontothere taxonomy; pp. 129–135 in S. G. Lucas, K. E. Zeigler, and P. E. Kondrashov (eds.), *Paleogene Mammals*. New Mexico Museum of Natural History and Science Bulletin 26.
- Mihlbachler, M. C., and L. T. Holbrook. 2008. The early Eocene Asian perissodactyl *Danjiangia pingi* and the origin of Brontotheriidae. *Journal of Vertebrate Paleontology* 27(3, Supplement): 115A.
- Mihlbachler, M. C., and T. Deméré. 2009. A new species of brontothere (Brontotheriidae: Perissodactyla: Mammalia) from the Santiago Formation, San Diego County, California. *Bulletin of the San Diego Natural History Museum* 41:1–36.
- Novacek, M. J., and J. A. Lillegraven. 1979. Terrestrial vertebrates from the later Eocene of San Diego County, California: a conspectus; pp. 69–79 in P. L. Abbott (ed.), *Eocene Depositional Systems*, San Diego. Geological Society of America, fieldtrip guidebook.
- Nixon, K. C., and K. C. Wheeler. 1990. An amplification of the phylogenetic species concept. *Cladistics* 6:211–223.
- Osborn, H. F. 1895. Fossil mammals of the Uinta Basin. *Expedition of 1894. Bulletin of the American Museum of Natural History* 7:71–105.
- Osborn, H. F. 1908. New or little known titanotheres from the Eocene and Oligocene. *Bulletin of the American Museum of Natural History* 24:599–617.
- Osborn, H. F. 1929. Titanotheres of Ancient Wyoming, Dakota, and Nebraska. *United States Geological Survey Monographs* 55:1–894.
- Qi, T., and K. C. Beard. 1996. *Nanotitan shanghuangensis*, gen. et sp. nov.: the smallest known brontothere. *Journal of Vertebrate Paleontology* 16:578–581.
- Peterson, G. L., and M. P. Kennedy. 1974. Lithostratigraphic variations in the Poway Group near San Diego, California. *San Diego Society of Natural History, Transactions* 17:251–258.
- Plavcan, J. M., and D. A. Cope. Metric variation and species recognition in the fossil record. *Evolutionary Anthropology* 10:204–222.
- Prothero, D. R. 2001. Magnetic stratigraphy of the middle Eocene Santiago Formation, San Diego and Orange counties, California; pp. 107–117 in D. R. Prothero (ed.), *Magnetic Stratigraphy of the Pacific Coast Cenozoic*. Pacific Section, SEPM, Book 91.

- Riggs, E. S. 1912. New or little known titanotheres from the lower Uintah formations with notes on the stratigraphy and distribution of fossils. *Field Museum of Natural History, Geological Series* 4:17–41.
- Robinson, P., G. F. Gunnell, S. L. Walsh, W. Clyde, J. Storer, R. K. Stucky, D. Froehlich, I. Ferrusquia-Villafranca, and M. C. McKenna. 2004. Wasatchian through Duchesnean biochronology of North America; pp. 106–155 in M. O. Woodburne (ed.), *Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology*. New York, Columbia University Press.
- Schieboub, J. A. 1977. Eocene *Perissodactyla* from the La Jolla and Poway groups, San Diego County, California. *Transactions of the San Diego Society of Natural History* 18:217–228.
- Sites, J. W., Jr., and J. C. Marshall. 2004. Operational criteria for delimiting species. *Annual Review of Ecology and Systematics* 35:199–227.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry*. W.H. Freeman and Company, New York, 887 pp.
- Stock, C. 1937. An Eocene titanotherium from San Diego County, California, with remarks on the age of the Poway Conglomerate. *Proceedings of the National Academy of Sciences of the United States of America* 23:48–53.
- Swofford, D. L. 2001. *PAUP\*: Phylogenetic Analysis Using Parsimony (\*and Other Methods)*. Version 4.0b10. Sinauer Associates, Sunderland, Massachusetts.
- Turnbull, W. D., and D. M. Martill. 1988. Taphonomy and preservation of a monospecific titanotherium assemblage from the Washakie formation (late Eocene), Southern Wyoming: an ecological accident in the fossil record. *Palaeogeography, Palaeoclimatology, Palaeoecology* 63:91–108.
- Via, S. 2001. Sympatric speciation in animals: the ugly duckling grows up. *Trends in Ecology and Evolution* 16:381–390.
- Walsh, S. L. 1991. Eocene mammal faunas of San Diego County; pp. 161–178 in P. L. Abbott and J. A. May (eds.), *Eocene Geologic History San Diego Region*. Society of Economic Mineralogists and Paleontologists, Pacific Section 68.
- Walsh, S. L. 1996. Middle Eocene mammal faunas of San Diego County, California; pp. 75–119 in D. R. Prothero and R. J. Emry (eds.), *The Terrestrial Eocene-Oligocene Transition in North America*. Cambridge University Press, New York.
- Walsh, S. L., D. R. Prothero, and D. J. Lundquist. 1996. Stratigraphy and paleomagnetism of the middle Eocene Friars Formation and Poway Group, southwestern San Diego County, California; pp. 120–154 in D. R. Prothero and R. J. Emry (eds.), *The Terrestrial Eocene-Oligocene Transition in North America*. Cambridge University Press, New York.
- Wheeler, Q., and R. Meier (eds.). 2000. *Species Concepts and Phylogenetic Theory: A Debate*. Columbia University Press, New York, 230 pp.
- Wheeler, Q. D., and N. I. Platnick. 2000. The phylogenetic species concept (*sensu* Wheeler and Platnick); pp. 55–69 in Q. D. Wheeler and R. Meier (eds.), *Species Concepts in Phylogenetic Theory: A Debate*. Columbia University Press, New York.
- Wilson, K. L. 1972. Eocene and related geology of a portion of the San Luis Rey and Encinitas quadrangles, San Diego County, California. Unpublished M.A. thesis, University of California, Riverside, California, 135 pp.
- Woodring, W. P., and W. P. Popenoe. 1945. U.S. Geological Survey, Oil and Gas Investigations Preliminary Chart 12.

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